
LATE CENOZOIC LIZARDS OF THE ANZA BORREGO DESERT, CALIFORNIA

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ABSTRACT. Late Neogene (Blancan and Irvingtonian) deposits from the Palm Springs Formation in Anza Borrego State Park (San Diego County, California, U.S.A.) have yielded the most diverse Tertiary lizard assemblage yet reported. Five lizard families are represented: Iguanidae, Xantusiidae, Scincidae, Teiidae, and Anguidae. The assemblages are taxonomically dominated by the Iguanidae, including *Gambelia corona* n. sp., *Dipsosaurus dorsalis*, *Pumilia novaceki** n. gen. et sp., which is the sister-taxon of *Iguana*, *Phrynosoma anzaense* n. sp., and two sceloporines not presently referable to genus. The morphology of the fossil *Dipsosaurus dorsalis* suggests that specimens of *Leiocephalus* described from the Neogene of continental North America may be referred to *Dipsosaurus dorsalis*. A new species of xantusiid, *Xantusia downsi**, is described. Several specimens, including all anguids and teiids, could be diagnosed to only general hierarchical levels.

Temporal faunal change took place during deposition of the Palm Springs Formation. Whereas the underrepresentation of some taxa in the lower part of the section may be due to sampling inconsistencies, the disappearance of the iguanine lineages roughly correlates with mammalian faunal turnover events.

The sparse fossil record of Neogene lizards hinders comparison among assemblages. In North America, other late Tertiary lizard assemblages are depauperate, consisting of a skink, a gerrhonotine, and one or two sceloporines. The Anza Borrego stratigraphic sequence contains all of these groups and additional taxa, making it the best indicator of late Tertiary lizard diversity yet surveyed.

SUMARIO. Los depósitos del período neogeno tardío (Blancano e Irvingtoniano) de la formación en Palm Springs en el Parque Estatal de Anza Borrego (en el condado de San Diego, California) han provisto los ejemplares más diversos hasta ahora recogidos de las lagartijas del período terciario. Aquí se encuentran cinco familias de lagartijas: los Iguanidae, los Xantusiidae, los Scincidae, los Teiidae y los Anguidae. La fauna está taxónomicamente dominada por los Iguanidae; estos incluyen *Gambelia corona* nueva especie, *Dipsosaurus dorsalis*, un nuevo género *Pumilia novaceki**, que se el grupo hermano al de los *Iguana*, *Phrynosoma anzaense* nueva especie y dos sceloporines a los cuales por el momento no se puede aludir como a un género. La morfología del *Dipsosaurus* indica que los especímenes del *Leiocephalus*, hasta ahora descritos como pertenecientes al neogeno de América del Norte continental, pueden referirse como del *Dipsosaurus dorsalis*. Un nuevo especie de Xantusiidae, *Xantusia downsi**, es descrito. Varios especímenes, inclusive todos los anguids y los teiids podrían ser únicamente definidos en niveles jerárquicos generales.

Algún cambio temporal en la fauna ocurrió durante el depósito de la Formación Palm Springs. Aunque la subrepresentación de alguna taxa en la parte inferior de la sección se deba a inconsistencias en la recaudación de ejemplares, la desaparición de los lineajes de Iguanine se puede relacionar con los eventos que transformaron la fauna mamífera.

Los escasos registros de fósiles de lagartijas del neogeno impide la comparación entre faunas. Otras faunas de lagartijas del período terciario son por lo general bastante pobres; consisten en un esquinco, y un gerrhonotine y uno o dos sceloporines. La fauna en Anza Borrego contiene todas estas formas y otras taxas adicionales, convirtiéndola en el mejor indicador de variedades de lagartijas del período Terciario que se haya investigado.

INTRODUCTION

Lizards of the North American southwestern deserts form a characteristic assemblage of taxa that is an important element of the modern fauna of the region. All extant families of North American

lizards are present in the region except Amphisbaenidae and Xenosauridae. Regional fossil and modern lizard assemblages are dominated by the taxonomically diverse Iguanidae. Little is known, however, of the history of the modern fauna.

Neogene lizard fossils are rare in southwestern North American fossil deposits. Only a few localities (Lindsay, 1972; Whistler, 1984; Harrison, 1972; Rogers, 1976; and others) have produced representative samples of fossil lizards, and many of these lack accompanying mammalian faunas and tight

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Table 1. Faunal list of lizard taxa from the Palm Springs Formation.

Iguanidae
<i>Dipsosaurus dorsalis</i>
<i>Pumilia novaceki</i> * n. gen. et metasp.
<i>Phrynosoma anazaense</i> n. sp.
<i>Phrynosoma</i> sp.
Sceloporine Type A
Sceloporine Type B
<i>Gambelia corona</i> n. sp.
Teiidae
<i>Ameiva/Cnemidophorus</i>
Teiini (basal)
Xantusiidae
<i>Xantusia downsi</i> * n. metasp.
Scincidae
<i>Eumeces</i> sp.
Anguidae
Gerrhonotinae indet.

stratigraphic control, or are represented by very fragmentary specimens. The presence of many lizard fossils from the Vellacito Badlands of Anza Borrego Desert State Park, San Diego County, California (Fig. 1), offers an exceptional opportunity to reconstruct Late Cenozoic regional lizard assemblages (Table 1).

Material used in this study was collected by field parties of the Natural History Museum of Los Angeles County, under the direction of Theodore Downs, from 1957 to the present. The fossil producing areas were originally prospected by Harley J. Garbani. Over 450 fossil localities have been collected through 4000 m of conformable sediments. The localities are stratigraphically tied to the type section of the Palm Springs Formation, which has been paleomagnetically correlated with the magnetic polarity timescale (Opdyke *et al.*, 1977).

Published work on the region's fossil assemblages has been incomplete. Downs and White (1968) reported the initial faunal list for the deposits documenting the rich mammalian fossils. Other reports have dealt with mammalian biostratigraphy (Opdyke *et al.*, 1977), species of the pocket gopher *Geomys* (White and Downs, 1961; Becker and White, 1981), the noctophyline bat *Anzanycterus anzaense* (White, 1969), and birds (Howard, 1963). Brattstrom (1961) provided the only account of the area's fossil herpetofauna in describing turtle plates as "referable to large tortoises." Previous to the present study, these same lizard specimens were studied by Richard Etheridge, George Callison, and Floyd Richey.

MATERIALS AND METHODS

Approximately 75 lizard specimens are catalogued into 75 numbered lots. Locality information is recorded by a

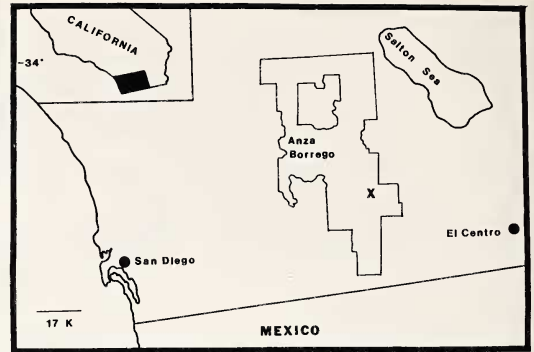


Figure 1. Location of Anza Borrego Desert State Park. Area of outcrops marked by an X.

number followed by a slash and the specimen number (locality number/specimen number). Stratigraphic position is fixed by "zone" numbers assigned to all fossil-producing localities, in reference to the type section. These zones refer to section thickness and are unrelated to section completeness (*sensu* Schindel, 1980) or faunal composition.

The use of metataxa (signified by an * following the Linnean binomial) follows that of Gauthier *et al.* (1988) as modified from Gauthier (1984), Donoghue (1985), and Mishler and Brandon (1987). Simply, a metataxon is a systematic unit whose monophyly is not established but contains some systematic information. Metataxa designate "suspect or unknown groups that can be considered separately as a general category of uncertain status. This includes unresolved groups for which there is no character evidence demonstrating that they are either monophyletic or paraphyletic" (Gauthier *et al.*, 1988). As used here, metataxa are specimens or groups of specimens that have apomorphic characters linking them with a monophyletic group; however, they lack unique apomorphic characters defining their monophyly. Metataxa display the character condition of an ancestor and their monophyletic sister-group; however, metataxa are not considered as ancestors here for reasons outlined in Schoch (1986) and Gaffney (1979). Because metataxa are recognized by branching pattern and represent the finest level of cladistic analysis, I use this convention only for metaspecies. Because species are the only natural units that can possibly be ancestral, metataxa may in some cases be more than phylogenetic artifacts. Recognition of metataxa at levels higher than the species is not recommended because these groups are of dubious monophyly.

Identification of fragmentary specimens at low taxonomic levels is problematic and often cannot be defended by reference to observable character states. Overinterpretation of the fossil record can lead to problems in analyzing temporal evolutionary and biogeographic patterns. If alpha-level systematics is used as a database for such studies, referral can only be made on the basis of derived characters (synapomorphies). The degree of hierarchical relationship specified for particular specimens is limited by the hierarchical level defined by characters preserved on each specimen. To allow maximum resolution, a hierarchical distribution of diagnostic characters must be established and used in diagnoses. This is especially the case when taxa have been diagnosed elsewhere on the basis of characters not preserved on the fossil specimens. Unfortunately, few lizard families have been analyzed cladistically to lower levels. Where such infor-

mation is not available, systematic decisions must be conservative.

In naming new taxa, I follow Gauthier *et al.* (1988), who suggest that taxonomic stability can be enhanced if widely used names are "restricted to clades in which at least two branches stemming from the basal node are represented by extant organisms." This approach renders the diagnoses of extant groups immune to change brought about by the description of new fossil material. For instance, *Pumilia novaceki** new genus and metaspecies, although very similar and closely related to species of the genus *Iguana* Laurenti, 1768, would require the rediagnosis of the extant genus *Iguana* if it were included therein. Such redefinition based on often fragmentary fossil material is less informative than diagnoses based on extant material, because it explains less information (*i.e.* character data). For the purpose of maximizing explanatory information and enhancing nomenclatural stability of commonly used names, the suggestions of Gauthier *et al.* (1988) are adopted herein. The taxonomy follows Estes (1983).

GEOLOGY

The Palm Springs Formation (Woodring, 1931) is exposed in the extensive Vallecito Badlands in the southern section of Anza Borrego Desert State Park. It is a thick unit (approximately 4000 m) that contains over 30 localities that have produced lizard fossils. The Palm Springs Formation is conformably overlain by the younger Canebrake Formation, a granitic gravel and boulder fanglomerate, and underlain by the older Imperial Formation, a predominantly marine unit composed of mud and sandstones with occasional biostromal oyster beds (Pappajohn, 1980). The Palm Springs Formation can be divided into four lithostratigraphic members, each indicative of a different regional depositional environment and varied source terrain. No lizard fossils are known from the conformable underlying marine Imperial Formation, although mammalian remains have been reported (Opdyke *et al.*, 1977).

Sediment composition varies both vertically and regionally. The presence of detrital Cretaceous foraminifera (Merriam and Bandy, 1965) indicates that some of the sediments, especially those lower in the section at the southeastern end of the park, were deposited by the ancestral Colorado River. Up-section and to the north, coarser materials derived from the rising Peninsular and Coast ranges to the west begin to replace the fluvial deposits. The sporadic presence throughout the section of an impoverished marine fauna indicates periodic intrusion of the Gulf of California into the area (Downs and Woodard, 1961).

Based on mammalian faunal associations, Downs and White (1968) divided the fossiliferous section into three local faunal zones independent of lithology. A lower Layer Cake local fauna has characteristic early Blancan affinities, the temporally intermediate Arroyo Seco local fauna is late Blancan in age, and the Vallecito Creek local fauna is late Blancan and early Irvingtonian. Age determination

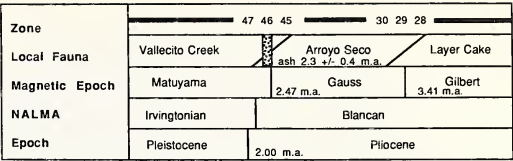


Figure 2. Stratigraphic markers in the fossil lizard-bearing portion of the Palm Springs Formation. Modified from Downs (pers. comm., 1986), Opdyke *et al.* (1977), and Harland *et al.* (1982).

of the Palm Springs sediments has been further refined by magnetostratigraphy (Opdyke *et al.*, 1977; Johnson *et al.*, 1983) (Fig. 2). The magnetic and paleontologic data gave slightly different results, indicating that the Layer Cake local fauna is Early Pliocene (early to middle Blancan), the Arroyo Seco local fauna is Middle Pliocene (middle Blancan), and the Vallecito Creek local fauna is Late Pliocene to Early Pleistocene (late Blancan to early Irvingtonian) (Downs, pers. comm., 1985).

SYSTEMATIC PALEONTOLOGY

Order Sauria McCartney, 1802

Suborder Lacertilia Owen, 1842

Infraorder Iguania Cope, 1864

Family Iguanidae Oppel, 1811

Subfamily Iguaninae Oppel, 1811

Pumilia new genus

DIAGNOSIS. Referred to a group containing *Iguana* and *Pumilia* on the basis of the synapomorphic presence of a ventral quadrate process of the squamosal and fan-shaped teeth with more denticles than most other iguanines (nine or more). Differs from *Iguana* in retaining primitive conditions, including a constricted basisphenoid and teeth with fewer denticles. The strict monophyly of the type species *Pumilia novaceki** cannot be established, as all pertinent characters are primitive for both *Iguana* and *Pumilia*.

TYPE SPECIES. *Pumilia novaceki**.

ETYMOLOGY. From Latin *pumila*, meaning diminutive. Referring to the small size of this lizard, compared to its close relatives.

*Pumilia novaceki** new metaspecies

Figure 3

DIAGNOSIS. The same as for genus.

HOLOTYPE. LACM 65116/13739.

REFERRED SPECIMEN. LACM 6661/78310.

TENTATIVELY REFERRED SPECIMENS. 6563/10600, 6661/78309, 6604/17651, 1922/10599.

ETYMOLOGY. In honor of my friend and colleague, Michael J. Novacek.



A



B

Figure 3. *Pumilia novaceki** n. gen. and metasp., holotype skull, LACM 13739 from LACM locality 65116. A, right lateral view; B, dorsal view. Bar = 4 mm.

DESCRIPTION OF THE HOLOTYPE. The holotype specimen (Fig. 3) is a well-preserved cranium and mandibles preserved in a fine-grained, highly indurated siltstone. The left side of the skull is crushed and laterally deformed. The braincase is separated and slightly offset from the rostrum. The dentaries and the ventral extensions of the quadrates are not preserved posteriorly. Several late ontogenetic features of *Iguana* (large prefrontal rugosity, mid-parietal ridge, and large, inflected angular process) are present. The mandibles are thick, heavy, and broken posteriorly; portions of the postdentary bones are present.

The dentary is deep and robust. Meckel's groove

is closed and fused, opening anterolingually as a small slot. The Meckelian reentrant tapers anteriorly and is filled dorsally by the coronoid, medially by the large splenial, and ventrally by the angular. An anterior mylohyoid foramen lies on the triangular, slightly concave splenial. The labial surface of the dentary is smooth with four mental foramina. Posteriorly, the dentary process of the coronoid overlaps the labial surface of the dentary.

Approximately 24 teeth are present on each dentary. Most of the teeth have been damaged by air-abrasive preparation or obscured by unremovable matrix and preservative. The leaf-shaped tooth crowns are compressed laterally and flare abruptly

dorsal to the level of the parapet. Four small cusps, or denticles, are arranged symmetrically on each side of the apical point.

The coronoid is thick, with a posteriorly deflected coronoid process that is rounded dorsally as in young *I. iguana* Linnaeus, 1758. The angular forms the ventral surface of the mandible posterior to the dentary. Anterolabially, it and the surangular contact the dentary along a "V"-shaped suture. The labial angular-surangular contact lies along a horizontal suture.

Dorsally, the mandible posterior to the dentary is formed by the surangular. Only the smooth, convex, labial surface is visible and it is broken posteriorly. Posteriorly, the mandibles are fragmented, but the distal extension of a large, inflected angular process is present medially.

The premaxilla is undivided and forms the anterior margin of the skull. The slender nasal process forms a convex arc inserting in an incised notch in the suture dividing the paired nasals, whereas the maxillary branch forms the anterior portion of the ventral shelf in the floor of the external nares. A single ethmoidal foramen lies just ventral to each narial opening. Seven weakly serrated, almost isodont, premaxillary teeth are present.

The maxillae are large, thick, and triangular, articulating anteriorly with the maxillary branch of the premaxilla, dorsally with the nasals, and posterodorsally with the prefrontals, lacrimals, and jugals. The nares are round and deeply excavated with the anterior inferior alveolar foramina lying on posterodorsally tapering concave shelves. Six supralabial foramina and approximately 22 teeth are present. Maxillary teeth are similar to those on the dentary.

Convex nasals form the posterodorsal border of the external nares. Paired nasal rugosities are present medially. The septomaxilla is inside the narial opening and is oriented almost vertically, attaching to the roof of the nasal capsule at the nasal premaxillary suture.

The frontal forms the dorsal border of the orbit along a thick, rounded supraorbital ridge. Supraorbital foramina lie on the lateroventral surfaces. The rectangular frontal widens posteriorly and is laterally concave above the orbits. Anteriorly, it forms an incised "M"-shaped suture with the nasals; anterolaterally it articulates with the prefrontals. The frontal-parietal suture is straight and contains the parietal foramen.

The anterior and dorsal perimeter of the elliptical orbit is bounded by three bones: a ventral jugal, a medial lacrimal, and a dorsal prefrontal. The crescent-shaped jugal is dorsoventrally concave; a strut-like posterior temporal process contacts the postorbital but not the squamosal. Anteriorly, the prefrontals are thick and contact the small, angular lacrimals along horizontal sutures. At least four suborbital foramina lie on each jugal. Dorsal to the lacrimals, the prefrontals form the anterodorsal angles of the orbits and are curved, long, and taper

posteriorly. A large prefrontal rugosity lies just dorsal to the lacrimal prefrontal juncture.

The triangular postorbital bounds the orbit posteriorly. The postorbital articulates anteroventrally with the temporal process of the jugal and posteriorly with the squamosal along a sinuous suture. The postorbital and jugal do not contact. Dorsally, the postorbital is constricted. Its posterior margin is concave and borders the supratemporal fenestrae. Anterodorsally, a large tuberosity is present just ventral to contact with the postfrontal. The postorbital-parietal boundary is short and lies posterior to the frontal-parietal suture.

The postfrontal is small and splinter-like, lying along the junction of the postorbital, parietal, and frontal on the inside of the orbit at the postero-dorsal orbital angle.

The hourglass-shaped parietal forms the roof of the braincase. Paired anterior postorbital processes meet the postorbitals along the anterior edge of the supratemporal fenestrae. Posterior to the postorbital process the parietal is constricted. Broad, smooth, sloping surfaces form the medial boundary of the supratemporal fenestrae meeting along the midline to form a crest. Anteriorly, the crest divides and continues as ridges along the postorbital processes. Posteriorly, a deep notch is formed by the posterior extension of the supratemporal parietal processes.

The dorsally ridged, hook-shaped squamosals enclose the supratemporal fenestrae posteriorly. Squamosals do not contact the posterior processes of the jugals along the ventral postorbital margins. Posteriorly, the squamosals curve medially to connect with the supratemporals and the parietal. Ventral quadrate processes meet the tympanic crests of the quadrates. Only the triangular posterior surfaces of the supratemporals are visible, lying below the junction of the squamosals and the parietal. A narrow splinter-like process lies ventral to most of the parietal along the supratemporal fenestrae.

The quadrate is "C"-shaped with an enlarged anterolateral tympanic crest that meets the quadrate process of the squamosal and the other temporal bones at the cephalic condyle. The anterior surface of the bone is slightly convex dorsoventrally and broad and flat mediolaterally; its posterior margin is concave. Ventrally the quadrate is not preserved.

The basisphenoid and basioccipital meet in a transverse suture, defined by a small ridge just anterior to the sphenoccipital tubercles. Together these bones form the hourglass-shaped floor of the braincase. The basipterygoid processes extend anteroventrally to meet the pterygoids. The ventral surface of the basisphenoid is laterally concave, whereas the basioccipital is convex.

The pterygoid is large, with a broad, flat palatine process and a thin posteriorly oriented quadrate process. A blunt transverse process articulates with the ectopterygoid laterally. Posteriorly, the quadrate process is broken anterior to its connection with the quadrate. Pterygoid teeth are arranged on

a small, ovoid pedestal anteromedial to the transverse process, not in crescentic rows as in living *Iguana* spp.; however, this condition is found in *Ctenosaura* spp. Wiegman, 1828, and some species of *Cyclura* Harlan, 1824 (de Queiroz, pers. comm.).

DESCRIPTION OF REFERRED MATERIAL.

Only LACM 78310, a crushed skull, approximately the same size as the holotype, can be definitively assigned to *P. novaceki** due to the presence of an identical tooth morphology, a ventral squamosal process, and a constricted basisphenoid. Although the entire skull is crushed, the surangular and prearticular are well preserved. On LACM 78310, the left prearticular is connected anteroventrally with the surangular on a broad, flattened shelf. The lateral surface tapers posteriorly to the articular facet. Posteriorly, a well-developed retroarticular process with a large hook-shaped lingually inflected angular process is present. The angular and surangular lie anterior to the prearticular. Dorsally, the surangular expands and flattens posteriorly toward the articular facet. The ventrally labiolateral surface originates on the angular and continues posteriorly onto the prearticular.

DESCRIPTION OF TENTATIVELY REFERRED MATERIAL. The remaining material is referred to cf. *P. novaceki** on the basis of tooth morphology or a constricted basisphenoid. LACM 10600 is a dorsoventrally crushed skull of about the same size as the holotype. The skull is very incomplete in the region of critical diagnostic features; several features that undergo ontogenetic change are also not preserved. Nevertheless, the teeth are well preserved and identical to the tooth form of the holotype. Of interest are the seven conical premaxillary teeth that lack the faint serrations seen in other species of *Iguana*.

LACM 17651 and 78309 are both cranial remains of juvenile individuals. The much more complete LACM 78309 is a well-preserved, but weathered, skull that unfortunately was damaged during preparation. The skull has been laterally compressed, perhaps accentuating its high, domed appearance. The right side of the skull is better preserved than the left. The maxilla is flat and contains 15 teeth with the *P. novaceki** shape. The entire right mandible is preserved but the suture pattern is obscured. The basicranial region displays the hourglass morphology seen in the holotype.

LACM 17651 is a fragmentary specimen, represented by a posterior maxillary fragment with 12 teeth and a fragment of the jugal and ventral postorbital. The specimen is tentatively referred to *P. novaceki** because of the similarity of the teeth.

LACM 10599 is a medium-sized left dentary with a single preserved tooth. The dentary is tentatively allocated to *P. novaceki** on the basis of tooth morphology. The tooth is set in a wide dental gutter and has a long columnar shaft; the dental parapet is high and only one-half of the tooth shaft extends above the level of the parapet. The tooth crown morphology is identical to the holotype.

DISCUSSION. Members of the genus *Iguana* are large, neotropical members of the New World Iguanidae (Etheridge and de Queiroz, 1988). Two extant species are recognized: the widespread *I. iguana* and the Antillean *I. delicatissima* Laurenti, 1768 (Lazell, 1973). Fossils referable to the genus are known only from the Holocene deposits of Barbados (Swinton, 1937; Ray, 1964), Martinique (Hoffstetter, 1940, 1946), and the Late Pleistocene of Ecuador (Hoffstetter, 1970; Baez and Gasparini, 1977). Recent *I. iguana* reach their northern distributional limit at latitude 24°30' in the riparian gallery forests of Sinaloa, Mexico (Hardy and McDiarmid, 1969).

The presence of a derived iguanine that forms the sister-group of species of *Iguana* in the Anza Borrego deposit is unexpected because close relatives do not live regionally. A Central American origin for the iguanines has been postulated (Etheridge, pers. comm.), based on the distribution of related forms and the relative lack of differentiation of the group in South America.

Specimens from the Palm Springs Formation are referable to the group of iguanine iguanids on the basis of fan-shaped teeth with numerous small denticles, a closed and fused Meckel's groove, and a supratemporal that lies on the medial side of the supratemporal process of the parietal (de Queiroz, 1987). Furthermore, the material is derived relative to *Cyclura* spp. in sharing with *Iguana* spp. a ventral quadrate process of the squamosal and leaf-shaped teeth with five or more small cusps (although, as pointed out by de Queiroz (1987), this last feature may be a synapomorphy of a larger group because it occurs in some other iguanines).

De Queiroz (1987) indicated that the position of the supratemporal may be a synapomorphy for iguanines. In most iguanines, including *P. novaceki**, *I. delicatissima*, and species of *Cyclura*, the supratemporal is visible from the lateral side of the skull on the supratemporal process of the parietal. In adult *I. iguana*, however, the supratemporal is usually only visible in posterior view on the inside of the occipital process of the parietal.

The shape of the basisphenoid differs among the genera of living iguanines (Etheridge, 1964a; Boulenger, 1890). Typically, the element is constricted posterior to the basiptyergoid process (Fig. 4). This constriction is usually more extreme in *Cyclura* spp. (Fig. 4B, C) than in *Iguana* spp. In *I. iguana* (Fig. 4F) the basisphenoid is constricted only slightly behind the basiptyergoid process. An ontogenetic shape transformation alters the proportions of the basisphenoid, yet the basisphenoid remains broad even in large individuals. Juvenile *Iguana* spp. (Fig. 4D, E) possess thin flanges forming a rectangular, ventrally concave surface. During growth, the relative length of the basisphenoid decreases, and the basiptyergoid processes become thick and short, giving the basisphenoid a more constricted appearance. However, the transverse flanges remain. In *I. delicatissima*, the basisphenoid is somewhat more

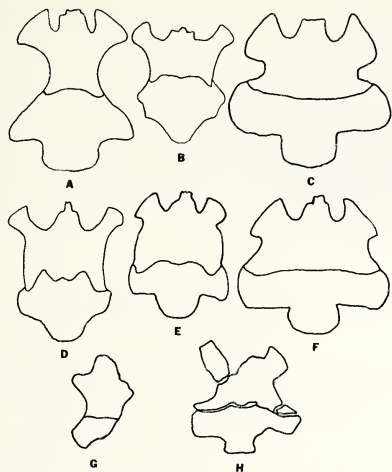


Figure 4. Basisphenoid-basioccipital plates of iguanines: A, adult *Ctenosaura pectinata* (Wiegman, 1834); B, juvenile *Cyclura nubila* (Gray, 1831); C, adult *Cyclura nubila*; D, hatchling *Iguana iguana* (Linnaeus, 1758); E, juvenile *Iguana iguana*; F, adult *Iguana iguana*; G, juvenile *Pumilia novaceki** n. gen. and metasp. (LACM 78309); and H, adult *Pumilia novaceki** (LACM 78310). Not drawn to same scale.

constricted, occasionally appearing as in some species of *Cyclura*, yet it is always wider than in *P. novaceki**. In all individuals of *Iguana* studied, the greatest constriction of the element forms a notch just posterior to the basiptyergoid process.

In *P. novaceki**, the basisphenoid is constricted, lacking flanges or notches posterior to the basiptyergoid process. The basiptyergoid processes remain long and thin during growth as in some *Cyclura* species. In juvenile cf. *P. novaceki**, the constriction is apparent (Fig. 4A), unlike *Iguana* spp. juveniles (Fig. 4D) where the basisphenoid is wide. The condition of a constricted basisphenoid is plesiomorphic for species of *Iguana* and *P. novaceki**.

The tooth form of *Iguana* spp. changes ontogenetically. In juvenile *I. iguana*, the teeth are small with flat, broadened tooth faces and approximately eight small denticles arranged four to a side. The tooth apex is formed by a small enlarged denticle (or cusp) closely associated on either side with an additional small denticle. The teeth are widely separated and the tooth crowns are non-overlapping. In large individuals, approximately 14 denticles are present and during ontogeny the teeth become broad and fan-shaped with overlapping tooth crowns. *Iguana delicatissima* displays a similar pattern, yet large adult individuals generally have teeth with fewer denticles than in *I. iguana* of comparable size. In *P. novaceki**, the teeth are similar to the condition in *I. delicatissima*. A similar condition is also found in some members of *Cyclura* species (Lazell, pers. comm.).

In *Iguana* spp. and *P. novaceki**, a ventral process on the squamosal abuts the tympanic crest of

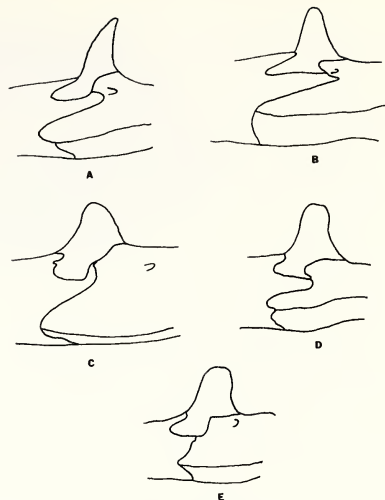


Figure 5. Labial view of medial mandibular elements in A) adult *Iguana iguana* (Linnaeus, 1758), B) juvenile *Iguana iguana*, C) adult *Cyclura nubila* (Gray, 1858), D) adult *Iguana delicatissima* Laurenti, 1768, and E) *Pumilia novaceki** n. gen. and metasp. (LACM 13739). Not drawn to same scale.

the quadrate laterally (de Queiroz, 1987). This feature is not present in other iguanines. Although in some *Cyclura* species the squamosal may touch the tympanic crest of the quadrate, only *Iguana* spp. and *P. novaceki** have distinct processes extending ventrally to the quadrate.

In *P. novaceki** the squamosal is long and narrow and hooks medially to meet the parietal anterior to the posterior skull margin. In all species of *Iguana*, *Cyclura*, and *Ctenosaura* Wiegman, 1828, the squamosal is short and relatively straight, extending diagonally to meet the parietal, supratemporal, and exoccipital anterior to the posterior margin of the skull. The amount of variation in this character within species of *Iguana* and *Cyclura* prompts one to question the phylogenetic worth of this feature and makes it difficult to justify using this feature as an autapomorphy of *P. novaceki**.

The surangular of *I. iguana* has a sharp dorsal ridge. In *P. novaceki**, *I. delicatissima*, and some *Cyclura* species the surangular is more smoothly rounded posterior to the coronoid and expands posterolaterally toward the articular facet. Shapes of the coronoid and dentary also vary within *Iguana* spp. and *P. novaceki**. In *I. iguana*, the coronoid is pointed dorsally (Fig. 5A, B) and the labial surface is divided by a vertical ridge. Ventrally, a process of the coronoid extends anteriorly to the posteriormost tooth. A small posterior process extends toward the anterior surangular foramen. In *P. novaceki**, *I. delicatissima*, and *Cyclura* spp. the coronoid is dorsally rounded, smoothly concave, and not ridged. In most adult members of *Cyclura* spp. and *P. novaceki**, a posterior process of the coronoid is absent. Additionally, in *I. iguana* and some

Cyclura species a posterior process of the dentary extends nearly to the anterior supranangular foramen (Fig. 5). In most *Cyclura* spp., *I. delicatissima*, and *P. novaceki** only a small posterior process of the dentary exists, if at all, and it does not extend posterior to the vertical axis of the coronoid.

Derived iguanines undergo an ontogenetic skull shape transformation. During growth, the jaw becomes deeper, the cranial sculpturing more pronounced, the angular process enlarges and hooks medially, and the adductor musculature fossae on the parietal enlarge and meet at the midline of the skull forming a sagittal crest. In *P. novaceki**, many of these features occur in smaller sized individuals than in *Iguana* spp. Although the distorted fossil material tempers statistical comparisons, in both *Iguana* species only individuals with a skull length of more than 55 mm have margins of the parietal adductor fossae meeting to form distinct crests. In *I. delicatissima* this crest forms earlier (as is indicated by relative size) than in *I. iguana* (relative to total skull length), forming a very tall, thin crest that is not as long as that in adult *I. iguana*. Initially this crest forms posteriorly and extends anteriorly, reducing the size of the parietal table. In *P. novaceki**, with a skull length of 58 mm, a complete sagittal crest extending the length of the parietal is present in two individuals, a condition not reached in *I. iguana* until approximately 70 mm of skull length is attained.

A large angular process is present on the holotype and LACM 78310, a feature developed to the same degree only in large adults of extant *Iguana* spp. The shape of this process varies among species of *Cyclura*, *I. iguana*, and *I. delicatissima*. In *I. delicatissima*, *Cyclura* spp., and *P. novaceki**, the angular process is hook-shaped and thin, extending medially from a relatively short retroarticular process that narrows posterolabially. Along the labial edge of the retroarticular process lies a scar for the adductor musculature. In *I. iguana* the retroarticular process is long, thin, and straight. The angular process is wedge-shaped in juveniles and becomes more hooked in adults but retains its wedge shape relative to the primitive hooked condition.

The jugal-squamosal contact on the ventral surface of the postorbital is ontogenetically variable within genera and species of iguanines. At the level of *Iguana* spp. + *P. novaceki**, however, this character appears useful. In *I. iguana* the jugal extends along the ventral surface of the postorbital and inserts in a notch formed by the anterior opening of the squamosal-postorbital suture line. In *I. delicatissima* the jugal tapers posteriorly and does not contact the squamosal, which abuts the postorbital along a straight dorsoventral suture. In *P. novaceki** the squamosal and jugal do not contact; both the jugal and squamosal taper along the ventral surface of the postorbital. Although no ontogenetic comparisons can be made between *P. novaceki** and *I. delicatissima*, this feature does not vary in *I. iguana* with growth. In *Cyclura* spp. and in other iguanines,

this character is variable, sometimes even on different sides of the same specimen.

Analysis of the characters of *P. novaceki** indicates that it is derived relative to *Cyclura* and other iguanines in having a ventral process of the squamosal. The absence of derived *Iguana* characters in *P. novaceki** easily differentiates it from species of *Iguana*; however, no characters define the strict monophyly of *P. novaceki**.

Dipsosaurus dorsalis Hallowell, 1854

Figure 6

REFERRED SPECIMENS. LACM 6831/20930, 6559/10598, 6552/78311, 65571/10604.

TENTATIVELY REFERRED SPECIMENS. 6525/19693, 6715/78213, 6583/78258, 6583/78259, 6583/78560, 6583/78261, 6583/78304.

DESCRIPTION. The material includes small jaw fragments with three teeth as well as complete crania and mandibles. The best specimen (LACM 20930) (Fig. 6) is a skull missing only part of the rostral and temporal regions. The skull measures 25.0 mm in length, comparable in size to extant adult *Dipsosaurus dorsalis*. The premaxilla is badly worn, the nasal process is missing, and no premaxillary teeth are preserved. The right maxilla contains 15 teeth in approximately 21 tooth spaces. The teeth are uniformly tricuspid with a large, blunt median cusp flanked by smaller, blunt cusps that flare laterally, so that they slightly overlap those of each adjacent tooth; the posterior cusp always overlaps the anterior cusp of the next posterior tooth. The largest teeth are posterior to the midpoint of the tooth row. The slightly bulbous tooth crowns taper to the width of the tooth shaft before they enter the dental parapet. Faint striations occur on the enamel of some teeth.

The parietal roof, although fractured, is roughly trapezoidal and flat. The pineal foramen lies within the frontal anterior to the frontoparietal suture (Fig. 6B). A small patch of teeth is present on the pterygoid, although much of the ventral skull surface is obscured by unremovable matrix.

The right mandible is more completely preserved than the left. The thick dentary is robust; Meckel's groove is closed and fused lingually. Anterolabially, a row of four evenly spaced mental foramina are present. The coronoid is "U"-shaped with an anterior ridge that originates in a large posterior fossa.

Another specimen of note (LACM 10604) is a semiarticulated bone mass including a vertebral region and limb and skull fragments. The teeth of this specimen are identical to the three-cusped teeth in the other fossil specimens. The vertebrae represent a presacral series. Each vertebra is elongate and robust, with zygantra and zygosphenes (Fig. 7B) that are connected by a thin crest. This condition is unique to *D. dorsalis*. In other iguanines the zygantra and zygosphenes are separated by a notch (de Queiroz, 1987).



A



B

Figure 6. *Dipsosaurus dorsalis* Hallowell, 1852, LACM 20930, from LACM locality 6831. A, left lateral view; B, dorsal view. Bar = 5 mm.

DESCRIPTION OF TENTATIVELY REFERRED MATERIAL.

The remaining referred material consists of bone masses that may be coprolites or owl pellets and isolated skull and dentary fragments. All of these specimens are associated with dental remains that display three- or, in one specimen, four-cusped teeth with overlapping tooth cusps.

DISCUSSION. *Dipsosaurus dorsalis* is a diurnal lizard of moderate size with a very high thermal optimum of 39°C (De Witt, 1967). Today *D. dorsalis* ranges throughout the southwestern United States and Sonora, Baja California, and Sinaloa, Mexico. The northern limit of this predominantly herbivorous lizard coincides almost directly with the boundary of the creosote forest community (Norris, 1953). The southern distribution of *D. dorsalis*, however, is not limited by the creosote community. In Mexico, *D. dorsalis* occurs well into arid subtropical scrub (Stebbins, 1954) habitats. *Dipsosaurus dorsalis* occupies the region of the fossil deposit today.

The only account of fossil *Dipsosaurus* is that

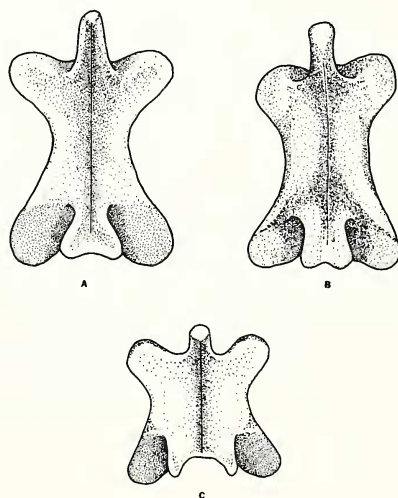


Figure 7. Presacral vertebrae of A) fossil *Dipsosaurus dorsalis* Hallowell, 1852 (LACM 10604) from LACM locality 6557; B) extant *Dipsosaurus dorsalis*; and C) *Leiocephalus melanocholorus*. Not drawn to same scale.

from the early Miocene Harrison Formation of Nebraska, originally described as *Tetralophosaurus minutus* (Olson, 1937).

De Queiroz (1987) listed eight cranial osteologic characters that are diagnostic of *D. dorsalis*. Of these, seven can be examined in the Anza Borrego fossil material, although not all on the same specimen. Only those specimens that have derived features restricted to *D. dorsalis* are positively referred to this species. The following discussion concerns characters that de Queiroz (1987) has presented as distinguishing synapomorphies of Recent *D. dorsalis*. An examination of these specimens within de Queiroz's phylogenetic framework demonstrates that only LACM 20930, 78311, 10598, and 10604 are diagnosable as *D. dorsalis*. Although other specimens show similarity to *D. dorsalis*, either the polarity of these uniting features cannot be determined, or the derived state of particular features is found in other taxa and is therefore of no use in referring these taxa to a particular species.

The presence of small, paired openings on the rostrum at the frontal nasal suture can be inferred to have been present on LACM 20930 and 78311. Although bones are not preserved in this region, impressions of these openings are present in the sandy matrix. The pineal foramen is preserved in similar fashion in LACM 10598; the cast indicates that it was entirely in the frontal. In LACM 20930 the frontal is preserved and includes the pineal foramen, the derived condition seen in Recent *D. dorsalis*.

In LACM 20930 the interior wall of the orbit indicates that the infraorbital foramen is not posteriorly bounded by a large process of the palatine. In LACM 20930 and 7831 the dorsal skull surfaces are exposed and the pterygoids "curve sharply toward midline anterior to the pterygoid notch" (de Queiroz, 1987), a derived condition found in most iguanines.

A single specimen (LACM 10598) preserves the retroarticular process as a mold. Recent *D. dorsalis* is unique among iguanines in displaying a retroarticular process that becomes quadrangular during ontogeny. In other iguanines, the tympanic and medial crests of the retroarticular process converge posteriorly giving adults of these species the primitive triangular-shaped retroarticular process (de Queiroz, 1987). The mold of the dorsal surface of the retroarticular process in LACM 10598 indicates that it shows the derived condition of a quadrangular retroarticular process as in large Recent *D. dorsalis*.

Dental features in the fossil specimens proved interesting. Surprisingly, only one of the fossil specimens exhibits more than three cusps on a single cheek tooth (Fig. 8B). Most extant *D. dorsalis* (Fig. 8A) have a combination of three- and four-cusped teeth, and four-cusped teeth are a synapomorphy and diagnostic character for the species (de Queiroz, 1987). Four-cusped teeth differ from the three-cusped (tricuspid) teeth in the addition of a small

accessory cusp lateral to either of the flared cusps. Only LACM 78261 has four cusps on a single tooth (Fig. 8B). The four-cusped condition found in most extant *D. dorsalis* usually occurs on all of the posterior teeth. A single four-cusped tooth, surrounded by tricuspid teeth, observed in the fossil specimen was never observed in extant specimens. Four-cusped teeth are present in juveniles and adults of extant *D. dorsalis*, as well as in the purported Miocene taxon *Tetralophosaurus minutus* Olson, 1937 (= *D. dorsalis*) (Estes, 1983). Only two out of 21 Recent individuals examined possessed tricuspid teeth exclusively. Three-cusped teeth may indicate that the Anza Borrego specimens fall outside the species *D. dorsalis* as diagnosed by de Queiroz or suggest that the ancestral iguanine and basal members of this clade were polymorphic for the presence of a fourth cusp (as in *Brachylophus* Cuvier, 1829) with the fourth cusp being present in all individuals of the iguanine crown group (except *Amblyrhynchus* Bell, 1825, and some *Ctenosaura*). This possibility was suggested by de Queiroz (1987).

Generally, extant *D. dorsalis* possess seven premaxillary teeth, although fewer or more may be present (Avery and Tanner, 1971). In iguanines, seven simply pointed or tricuspid premaxillary teeth is typical (de Queiroz, 1987) although variation occurs. LACM 78311, the only specimen with a complete component of premaxillary teeth preserved, has six simple, conical teeth, a condition found in 23% of the available sample of extant *D. dorsalis* examined by de Queiroz (1987).

The Anza Borrego specimens all have pterygoid teeth. Although the loss of these has been used as a derived feature in diagnosing extant *D. dorsalis* (Etheridge and de Queiroz, 1988; de Queiroz, 1987), pterygoid teeth are occasionally present in Recent specimens. Although the Anza Borrego material differs in detail from most living *D. dorsalis*, the amount of variation present in extant populations limits the diagnostic value of the differentiating characters; hence, the Anza Borrego fossils are assigned to the living species.

Reexamination of other Tertiary lizards raises some perplexing questions, and may, on closer inspection, indicate additional fossil occurrences of *D. dorsalis*. For example, Wellstead (1982) described *Leiocephalus nebraskensis* Wellstead, 1982 (= *Leiocephalus septentrionalis* Wellstead, 1983), from the Miocene Valentine Formation of Nebraska. In discussing the relationships of *L. nebraskensis*, Wellstead states, following Estes (1963a) and Etheridge (1965, 1966), that it is "comparable only to the dentaries of *Leiocephalus* and *Liolaemus* in the common possession of a fused Meckelian groove, a scar representing the anterolabial process of the coronoid bone, and tricuspid teeth" (Wellstead, 1982:367). All of these features are found to some extent in *D. dorsalis* and the fossil material described here. Generally, the labial anterior process of the coronoid in *D. dorsalis* does not extend past the last posterior tooth. In some individuals

(Fig. 9A), the extension is identical to that seen in *L. nebraskensis* (Fig. 9B) and some extant *Leiocephalus* (Fig. 9C). The tricuspid cheek teeth of the Anza Borrego material is identical to some extant *D. dorsalis* and many *Leiocephalus* species (Pregill, 1981; pers. obs.).

Mandibular features also suggest that *L. nebraskensis* may be referable to *D. dorsalis*. In most *Leiocephalus* species, tricuspid teeth first appear posterior to the seventh dental space (Pregill, 1981), rather than in spaces two through four as in *D. dorsalis*, or four or five as in *L. etheridgei* (Pregill, 1981), *L. cuneus* (Etheridge, 1964a), or *L. nebraskensis* (Wellstead, 1982). Additionally, published figures of *L. nebraskensis* (Wellstead, 1982; pers. comm.) indicate a posterior extension of the dentary only slightly posterior to the vertical axis of the coronoid as in iguanines (Figs. 5, 9). In extant *Leiocephalus* spp. and other tropidurine iguanids examined, the posterior extension of the dentary extends well back onto the surangular, posterior to the coronoid axis (Pregill, 1981). Also in extant species of *Leiocephalus* and other tropidurines, the anterior lingual surface of the dentary below the tooth row is shallow and rounded (Robinson and Van Devender, 1973). In *D. dorsalis* and, as indicated in Wellstead's figure 1, *L. nebraskensis*, this surface is flat and deep (Wellstead, 1982:366).

Other reports of Tertiary *Leiocephalus* species from mid-continental North America also are questionable. Much of the material (Robinson and Van Devender, 1973; Setoguchi, 1978) is too incomplete for a confident identification based on diagnostic characters. Other material (Holman and Sullivan, 1981; Wellstead, 1982) referred to *Leiocephalus* spp. cannot be distinguished from some extant *D. dorsalis* and the fossil material from Anza Borrego. The single record that I consider valid evidence for a continental North American tropidurine is that from the Early Miocene Thomas Farm local fauna of Florida (Estes, 1963a). This specimen has the *Leiocephalus*-like features of small foramina in the cementum between the dentary teeth, a fused Meckelian groove, and a shallow, rounded dentary surface ventral to the tooth row. Ultimately, the definitive confirmation of North American mid-continental *Leiocephalus* species awaits better fossil material, because the genus can easily be diagnosed with skeletal material (Etheridge and de Queiroz, 1988).

Crotaphytine group
sensu Etheridge and de Queiroz, 1988

Gambelia Baird, 1859

***Gambelia corona* new species**

Figure 10

DIAGNOSIS. Shares with other crotaphytine species the derived loss of a prefrontal, the presence of a boney labyrinth whose outlines are visible on the dorsolateral surface of the posterior braincase,

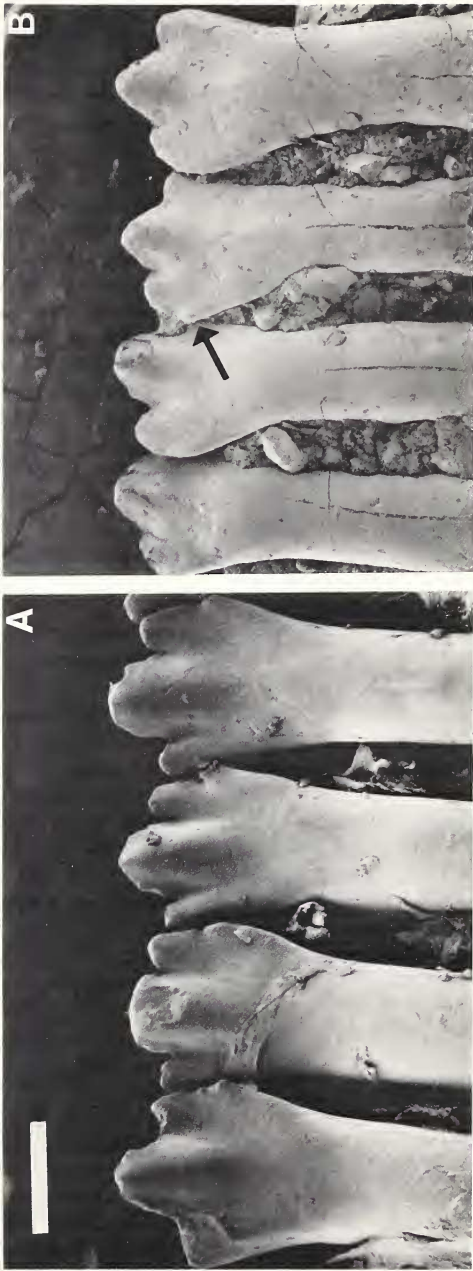


Figure 8. Dentary teeth of *Diposaurus dorsalis*. A, extant *Diposaurus dorsalis*; B, LACM 78261 from LACM locality 6583. Anterior toward center. Note development of accessory cusps in recent specimen and single accessory cusp in LACM 6583/78261. Bar = 0.5 mm.

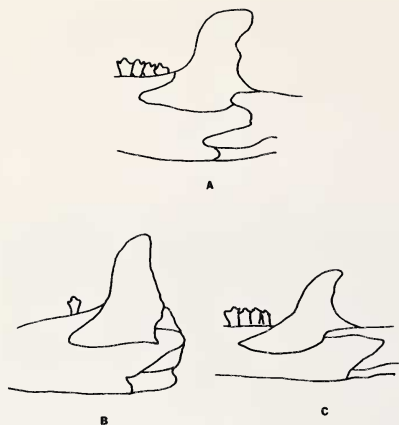


Figure 9. Mandibles of *Dipsosaurus dorsalis* and *Leiocephalus*. A, extant *Dipsosaurus dorsalis*; B, *Leiocephalus nebraskensis* Wellstead, 1982 (modified from Wellstead, 1982); and C, extant *Leiocephalus carinatus* Gray, 1852.

an elongate dentary (from Etheridge and de Queiroz, 1988), and the possession of posterior teeth with flared tooth cusps and sharp, recurved, unicuspid anterior teeth. *Gambelia corona* is a member of the genus *Gambelia* due to the shared derived presence of a Meckel's groove that is fused for more than half its length anterior to the splenial, an extremely heterodont tooth condition and a posteromedial process of the coronoid that is oriented posteroventrally. Furthermore, *Gambelia corona* has a frontal that is wider than that of other crotaphytine species and is transversally concave with supraorbital ridges, rather than flat. It can be further distinguished from other species by the unique derived presence of a frontoparietal suture anterior to the posterior extension of the orbits rather than even with the postorbital bar as in other crotaphytine species.

HOLOTYPE. LACM 7058/42880, a cranium and mandibles.

ETYMOLOGY. From Latin *corona*, meaning crown, referring to the distinguishing features of the frontal.

DESCRIPTION OF THE HOLOTYPE. Triangular in shape, the skull measures 29.2 mm in length, which is within the range of large members of extant crotaphytine species. Fused, indistinct sutures and superficial sculpturing indicate that the specimen is an adult.

The mandibles are shattered posterior to the dentary. Anteriorly, the dentary is long and thin with six mental foramina. Most of the splenial is obscured by matrix, but its anterior process fills Meckel's groove, which is closed and unfused for most of the length of Meckel's groove. Labial surfaces of the coronoids are not preserved. Lingually, the coronoid extends posteroventrally onto the surangular and angular.

The angular is shattered. On the mandible, a dor-

sal ridge runs between the coronoid and the articular, as in *Gambelia* spp. Ventrally, the surangular expands into a flattened surface that continues posteriorly into the articular. The angular process, although broken, appears to have been inflected. The articular condyle is broad and flat and is flanked by a medial process that rises as a protuberance on the ventral side of the mandible. Posteriorly, the articular is not preserved.

The premaxilla contains seven conical, isodont teeth. The nasal process is short and thick, as in *C. collaris* Say, 1823, and forms the anterodorsal border of the rounded external nares. The nasal process arches above the outline of the skull as in other *Gambelia* species.

The maxillae are triangular and slightly concave, although not as concave as in adult *G. wislizenii*. At least 22 teeth are present. The five posterior teeth are tricuspid, with a large median cusp and recurving tooth shafts. Anterior teeth are isodont, sharp, and recurved, extending 1.1 mm above the maxillary parapet. Five supralabial foramina are present. The ventral rim of the external nares are flattened shelves that widen anteriorly at the maxilla-premaxilla contact.

Prefrontals and nasals contact the frontal via a "W"-shaped suture. The triangular prefrontals abut the frontal along a straight suture that extends posterior to the middle of the orbits. A prefrontal knob lies on the anterodorsal angle of the orbits, and a shallow concavity lies at the median naso-frontal contact. The faintly sculptured nasals arch posteriorly. Their median contact is short, divided anteriorly by the nasal process of the premaxilla.

A laterally concave frontal forms the dorsal border of the orbits along well-developed supraorbital ridges. Posteriorly, it contacts the parietal anterior to the posterior margin of the orbits, a condition found in no other crotaphytine species examined. The parietal foramen lies on the frontoparietal suture. As in extant crotaphytine species, postfrontals are absent.

The jugal and lacrimal (the latter preserved only as fragments and matrix impressions) form the anterior and ventral margins of the orbits. The jugal is crescentic and articulates ventrally with the maxilla, sweeping posterodorsally to contact the postorbital. Several suborbital foramina and a small postorbital rugosity are present. Neither squamosal is complete; only the posterior-most contacts with the quadrate, supratemporal, and parietal are preserved. The supratemporal is narrow and wedge-shaped, lying between the squamosal, the paraoccipital process of the exoccipital, and the quadrate.

Fragments of the scleral ossicles are preserved within the right orbit.

The parietal forms the dorsal and lateral boundaries of the supratemporal fenestrae. The anterolateral processes taper to meet the postorbitals at the postorbital bars. Posteriorly, the parietal contacts the supratemporal and squamosal. Between the squamosal processes, the supraoccipital meets



Figure 10. *Gambelia corona* n. sp., holotype skull, LACM 42880 from locality 7058. **A**, left lateral view; **B**, dorsal view. Bar = 5 mm.

the parietal table. The dorsal surface of the parietal is concave.

The supraoccipital has a medial, longitudinal crest and slopes gradually posterior, dorsal to the foramen magnum as in other *Gambelia* species. The outlines of the boney labyrinth of the ear are visible laterally. The paroccipital process is long and hourglass-shaped; laterally it abuts the squamosal. A shallow, medial, longitudinal groove extends approximately half the length of the process, just lateral to the braincase.

The quadrate is "C"-shaped. Dorsally it contacts the paroccipital process, the supratemporal, and the

squamosal. On the posterior quadrate surface, a large concavity, bordered by the tympanic crest, tapers toward the ventral condyle.

The basioccipital and basisphenoid are fused into an hourglass-shaped unit. Paired sphenoccipital tubercles are present laterally; anteriorly a pair of thick basipterygoid processes reach anteroventrally to the pterygoids. Between the basipterygoid processes lies a parasphenoid process.

The pterygoids are largely concealed by unremovable matrix, yet a single row of small pterygoid teeth are present on a longitudinally extending ridge along the medial pterygoid boundary. Posteriorly

this ridge flattens as the pterygoid narrows anterior to articulation with the ectopterygoid.

Anterior to the pterygoids lie the palatines, which display small palatine teeth in a shallow depression.

DISCUSSION. Crotaphytine species are well known from western North American Pleistocene deposits (Etheridge, 1958; Holman, 1970; and others). Most of the material has been referred to *C. collaris*. Fossil occurrences of *G. wislizenii* (Baird and Girard, 1852) are restricted to the Holocene in the southwestern deserts (Van Devender and Mead, 1978; Van Devender and Worthington, 1978; Brattstrom, 1958; Norell, 1986). Holman (1972) described the Early Oligocene *C. oligocenicus*, from Saskatchewan, Canada, on the basis of fragmentary material. This species has several very primitive iguanid features, and its reference to *Crotaphytus* is questionable (Estes, 1983). The presence of Pliocene *G. corona* in California marks the earliest undisputable occurrence of the genus and of the group.

Within the crotaphytines, two diagnosable generic groups have been recognized (Weiner and Smith, 1965; Etheridge and de Queiroz, 1988), although this suggestion has been somewhat controversial (Montanucci *et al.*, 1975; Montanucci, 1969). The genus *Crotaphytus* contains three species: *C. collaris*, *C. reticulatus* Baird, 1858, and *C. insularis* Van Denburgh and Slevin, 1922, and the genus *Gambelia* contains only *G. wislizenii* and *G. silus* (Stejneger, 1893). Many workers consider *G. silus* a subspecies of *G. wislizenii*. Etheridge and de Queiroz (1988) provided a diagnosis for the group and the two genera. Although the characters that these authors present in support of the monophyly of these groups cannot all be considered exclusively apomorphic at this level (due to a lack of resolution of outgroup taxa), they state that "the unity of the crotaphytine group is not controversial" and that "Both *Crotaphytus* and *Gambelia* possess derived characters supporting their separate monophyly" (Etheridge and de Queiroz, 1988:322).

Whereas *G. corona* differs from all other crotaphytine species in diagnostic characters, it shares several features with other *Gambelia* species. The nasal branch of the premaxilla in *Crotaphytus* spp. conforms to the outline of the rostrum. In species of *Gambelia* (including *G. corona*) the nasal process arches, protruding dorsally in lateral view from the skull outline. The external nares of *G. wislizenii* are more ovoid and elongate than those of either *G. corona*, *G. silus*, or *C. collaris*, and this may be a synapomorphy of the species. However, comparative material for *G. silus* was very limited.

In species of *Crotaphytus*, the dorsal surface of the surangular is expanded and flat, with the opening to the suprangular foramen directed almost vertically in a shallow depression between two faint longitudinal ridges. Posteriorly, a prearticular process hooks lingually anterior to the articular condyle. In *Gambelia* species the dorsal surface of the surangular is ridge-like with no dorsally flattened surface, and there is a labially directed anterior sur-

angular foramen. Also in *Gambelia*, a narrow shelf of bone connects the entire lingual prearticular process with the surangular, forming a posterolingual shelf that expands posteriorly to the articular condyle making the prearticular process less distinct than in species of *Crotaphytus*. In species of *Gambelia* the ventral extension of the coronoid on the inside of the jaw onto the angular and surangular occurs in a posterior arc, whereas in *Crotaphytus* spp. the extension is almost vertical.

Much discussion has centered on the dental morphology of crotaphytine species. Weiner and Smith (1965) indicated that the condition found in *G. wislizenii* (including *G. silus*) is heterodont, with anterior haplodont, median diconodont, and posterior triconodont (their terminology) teeth grading into each other. *Crotaphytus collaris* exhibits a subheterodont condition. Robinson and Tanner (1962) noted that the teeth of *G. wislizenii* are narrower and longer than the broad, short teeth found in the 'collaris' group. Montanucci (1969) disputed these conclusions by pointing out that these categories are subjective, influenced by ontogeny, and contain intergradational forms. Nevertheless, while intermediates between the heterodont and subheterodont conditions are found, the sharp, recurved anterior teeth found in most *G. wislizenii* are never developed to the same degree in species of *Crotaphytus*. Only the maxillary teeth (the dentary teeth are hidden by unpreparable matrix) of *G. corona* are sufficiently free of matrix to allow inspection. *Gambelia corona* has 22 teeth, compared with 17 to 22 teeth in *G. wislizenii* and 14 to 20 in *Crotaphytus* species (Weiner and Smith, 1965). The size, cusp pattern, and recurved aspect of the fang-like anterior teeth and triconodont posterior teeth in *G. corona* approximate the condition seen in *G. wislizenii* and *G. silus*, and like the arched premaxillary process, is suggestive of a sister-group relationship.

The frontal of *G. corona* is wider than any other crotaphytine species observed and has a pair of supraorbital ridges along the dorsal border of the orbits, giving the frontal a laterally concave aspect. Some adult *C. collaris* display slightly concave frontals; the supraorbital ridges, however, are never as well defined as in *G. corona*. Some other iguanids acquire concave frontals late in ontogeny, and some also show supraorbital ridges. This feature may simply be a coincidence of large size and a wide frontal, but because it is not seen in other crotaphytine species, it is considered here to be derived.

The repositioning of the frontoparietal suture is perhaps correlated with a widening of the frontal. In other iguanids, the frontoparietal suture lies behind the posterior angle of the orbits, abutting the postorbital bar. In *G. corona* the frontoparietal suture lies along the posterodorsal border of the orbit, anterior to the postorbital bar.

The basisphenoid in *C. collaris* articulates with the basioccipital in a long, straight transverse suture. In *G. wislizenii*, branches of the basisphenoid ex-

tend posteriorly to the sphenoccipital tubercles of the basisphenoid. This condition also occurs in sceloporines, iguanines, and morunasaurines. *Gambelia corona* displays the condition seen in *C. colaris*.

My decision to retain the name *Gambelia* for this species may seem to be a violation of the principles for naming taxa described in the methods section. Here my intention is to not cause a proliferation of names. Because I cannot demonstrate that the two recent *Gambelia* species form a monophyletic group independent of *G. corona*, it seems pointless to assign this species to a new genus at this time. In the event that *G. corona* is found to be the sister-group to these species it should be placed in a new, as yet unnamed, genus.

Sceloporine group
sensu Etheridge and de Queiroz, 1988

Phrynosoma Wiegmann, 1828

***Phrynosoma anzaense* new species**

Figure 11

HOLOTYPE. LACM 6822/64595.

DIAGNOSIS. Shares with all other *Phrynosoma* species parietal and squamosal cranial horns. Shares with *P. mcalli* the derived presence of a supratemporal fenestra that is constricted by flanges from the surrounding bones. Differs from all other *Phrynosoma* by possessing accessory horns ventral to the largest squamosal horn.

ETYMOLOGY. In reference to the type locality in the Anza Borrego desert.

DESCRIPTION OF THE HOLOTYPE. LACM 64595 is a posterior skull region in a poorly indurated sandstone nodule (Fig. 11). The parietal, left squamosal, and left postorbital are the only complete dorsal skull elements. The left jugal, frontal above the orbit, prefrontal, and right postorbital are present but broken. The basioccipital and basisphenoid are the only basicranial elements present.

The prefrontal is roughly triangular. The antero-medial surface is not broken, but detached from the nasal and frontal along the suture joint. Laterally, an extensive supraorbital process sweeps posteriorly forming the dorsal rim of the orbit. In some *Phrynosoma* species this process meets the supraorbital process of the frontal forming a supraciliary rim. Because the prefrontal has been rotated diagonally, this association cannot be examined in LACM 64595; the supraorbital process is large, however, compared to most other *Phrynosoma* species examined. Anterior to the supraorbital process the orbital rim plunges ventrally to an assumed, but missing, contact with the maxilla. Sculpture, in the form of small rugose protuberances, is present along the dorsal orbital rim.

The frontal is incomplete. Anterior to the frontoparietal suture the frontal is broken into right and left components. The frontoparietal suture ex-

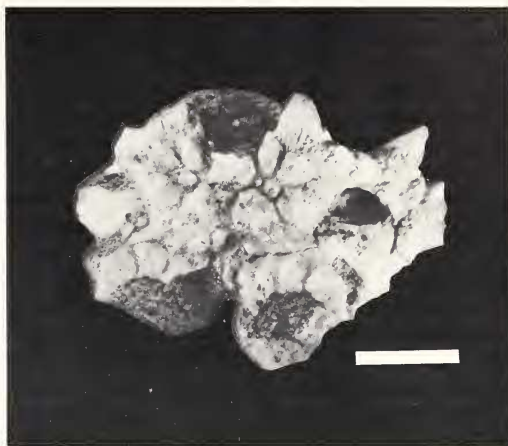


Figure 11. Cranium of *Phrynosoma anzaense* n. sp., LACM 64595 from LACM locality 65116. Bar = 5 mm.

tends from the posterior angle of the orbits through the pineal foramen. Although broken, a thick supraorbital process extends forward on top of the diagonally rotated supraorbital process of the prefrontal. The frontal margin along the supratemporal fenestra is covered with rough tubercles. A large horn lies at the posterolateral border of the bone above the posterior angle of the orbits. The broad, flat area between the orbits is covered with rugose tubercles.

The hourglass-shaped postorbital abuts the frontal and parietal dorsally, and the jugal and squamosal ventrally. The arched anterior surface forms the posterior margin of the skull. The nearly vertical posterior surface borders the anterior limit of the semicircular supratemporal fenestrae. The surface of the postorbital is sculptured with small granular tubercles.

The fragmentary jugal forms part of the ventral orbital margin. Two small horns occupy the laterally oriented face of the bone. One lies in the wide area directly below the postorbital bar. Anterior to the posterior angle of the orbit, a second, better defined horn lies near the orbital rim. Just ventral to these horns the jugal is broken.

The heavily sculptured squamosal forms the posterolateral border of the skull. Along the lateral squamosal border, three unequally sized horns point posterolaterally. The two anterior horns are broken distally but have joined bases. Judging from relative base size, the anteriormost horn appears to have been smaller than the median or posterior horn. The jugal-squamosal suture lies just anterior to the base of the anterior squamosal horn. The posterior horn is largest and is separated from the anterior pair of horns by a short diastema. The apex of the posterior horn projects posteriorly; its dorsal and ventral surface is sculptured and striated. The squamosal and parietal form the posterior margin of the cranium. Medial to the posterior squamosal horn lies the suture where the squamosal abuts the pa-

rietal. The thin, flat interior surface of the squamosal forms half of the curved posterior border of the supratemporal fenestrae. The dorsal squamosal surface is covered by large tubercles. Dorsal and ventral large single tubercles lie both between the single posterior and paired anterior horns and at the postorbital, jugal squamosal suture. Although the ventral surface of the squamosal is poorly preserved it apparently lacks sculpture.

The parietal forms the dorsal roof and posterior margin of the specimen. It is a large, rugose, roughly triangular bone with a pair of horns emanating from its posterolateral border. These horns are broken just distal to their bases. Larger than the squamosal horns, these parietal horns are also sculptured and have striations running along their axes. Between the horns a small spine on a tubercle projects posteriorly. The pineal foramen is a "U"-shaped notch in the parietal at the frontoparietal suture. The parietal margin of the supratemporal fenestra is formed of very thin bone. The parietal bar contacts the squamosal lateral to the large parietal horns and a small accessory horn that is located on a large tubercle on the lateral base of the main horn. Two other tubercles ring the base of each parietal horn. The entire dorsal surface of the parietal is heavily sculptured, with a prominent group of four tubercles in a transverse "V"-shaped row just posterior to the pineal foramen.

The only basicranial elements preserved are the basisphenoid and basioccipital. The latter is compressed longitudinally with a large occipital condyle posteriorly and a pair of smooth sphenoccipital tubercles laterally. The suture between the basioccipital and basisphenoid lies anterior to the sphenoccipital tubercles. The basisphenoid is transversally concave and tapers from posterior to anterior. Two basiptyergoid processes extend anteriorly from the anterior margin of the basisphenoid.

DISCUSSION. The most recent review of extant *Phrynosoma* recognizes 14 species (Montanucci, 1987). Estes (1983) listed an additional three fossil species from the Neogene of western North America. Montanucci's review allows *P. anzaense* to be evaluated within a comparative framework.

Several features of the jugal were considered to be phylogenetically informative by Montanucci and therefore may aid in determining the phylogenetic affinities of *P. anzaense*. The posterior border of the jugal in *P. anzaense* is expanded posteriorly, and the jugal surface is covered with tuberosities. Montanucci considered this condition derived for a group composed of the species *P. modestum* Girard, 1852, *P. platyrhinos* Girard, 1852, *P. mcalli* (Hallowell, 1852), *P. solare* (Gray, 1845), *P. cornutum* Harlan, 1825, *P. coronatum* Gray, 1857, *P. orbiculare* (Linnaeus, 1651), and *P. douglassi* Girard, 1858. Furthermore, *P. anzaense* shares with all of these taxa, except *P. douglassi* and *P. orbiculare*, a jugal with an anteriorly sloping posterior border and a jugal surface with tuberosities. Apparently, Montanucci considered that the processes

were a continued transformation of jugal rugosities, although this is not made explicit. *Phrynosoma anzaense* shares with *P. solare*, *P. mcalli*, *P. platyrhinos*, and *P. modestum* an enlarged scale at the base of the parietal horn.

Except for *P. mcalli* and *P. anzaense*, all horned lizards have relatively large, ovoid supratemporal fenestrae. In no case is the width of the posttemporal bar nearly as wide as the anteroposterior width of the supratemporal fenestrae in *P. anzaense* and *P. mcalli*. In the latter, outgrowths from the parietal, frontal, and postorbital bones almost, or sometimes completely, cover the supratemporal opening, a feature responsible for its original placement in the monotypic genus *Anota* (Hallowell, 1852). Only in *P. anzaense* and *P. mcalli* do flanges of bone extend into the supratemporal fenestrae from the entire circumference of the fenestrae, resulting in a constriction of the opening. The condition found in *P. anzaense* is not as well developed as in any *P. mcalli* examined. In addition, no *P. mcalli* examined showed the degree of development of cranial sculpture found in *P. anzaense*. My initial analysis (Norell, 1983) of the *P. anzaense* condition as less constricted than *P. mcalli* was questioned by Montanucci (1987), who suggested that this may simply represent the condition found in early ontogenetic stages of *P. mcalli*. However, because the type specimen of *P. anzaense* represents a mature individual (as can be determined by the degree of cranial sculpture, the extensive development of cranial horns and the degree of fusion of the cranial sutures), I doubt that this is the case.

Because the pattern of squamosal horns is used in the diagnosis of *P. anzaense*, the distribution of this feature among *Phrynosoma* species is discussed. This feature was not used by Montanucci as a phylogenetic character. However, due to the extensive phylogenetic variation seen in this feature it may be of phylogenetic and diagnostic value. The relative size and number of squamosal horns varies among species of *Phrynosoma*. *Phrynosoma asio* Cope, 1864, possesses two large posteriorly directed horns on each squamosal. Two or three squamosal horns are present in *P. coronatum* and *P. douglassi* Girard. In *P. asio* the bases of the horns are separate. At the anterior base of the anterior squamosal horn, a very small accessory horn is variably present along the squamosal jugal suture. In juvenile *P. coronatum*, horns with separate bases are present. During ontogeny, the horn bases join. In large individuals a pair of small rugose accessory horns are present; one of these small pointed horns lies dorsal and posterior to the base of the posterior squamosal horn, and the other dorsal to the junction of the large horn bases. *Phrynosoma cerroense* (Stejneger, 1893) and *P. taurus* Duges, 1864, apparently also have two squamosal horns (Presch, 1969) and *P. ditmarsii* Stejneger, 1907, possesses four squamosal horns. Specimens of these species were unavailable for study.

Most species of horned lizards display a pattern

of three sagittally aligned squamosal horns, and in all cases the anterior horn is smaller than the two posterior horns. In *P. mcalli* and *P. cornutum*, the two posterior squamosal horns are large and approximately equal in size, but in *P. platyrhinos* the horns increase in dimension posteriorly. *Phrynosoma orbiculare* has an anterior small squamosal horn, a short median horn expanded at its base, and a long posterior horn with a constricted base. All squamosal horns are evenly spaced in *P. platyrhinos*, *P. orbiculare*, and *P. mcalli*. In *P. cornutum* and *P. douglassi*, the anterior two horns are joined at their bases. Dorsal accessory horns, like those in *P. coronatum*, are present in *P. mcalli*, *P. cornutum*, and *P. orbiculare*. Horned lizards with three squamosal horns that were not available for this study were *P. boucardii* and *P. braconieri* (Presch, 1969).

The diminutive *P. modestum* and the large *P. solare* both possess four squamosal horns. In *P. solare* these horns are large, joined at the bases, and increase in size posteriorly. In *P. modestum* the two anterior horns are large, although not as large as the posterior horn and joined at their bases. The third posterior horn is very small, lying in between the bases of the second and fourth posterior horns. Identification of this horn may be the reason for the discrepancy between my observation of four horns and Montanucci's (1987) observation of three. Neither *P. solare* nor *P. modestum* possess small ventral accessory horns. The unstudied *P. ditmarsii* is reported to have three squamosal horns (Montanucci, 1987).

Phrynosoma anzaense has three large horns on its squamosal, a common pattern in other *Phrynosoma* species. The anterior horns of *P. anzaense* are fused at the base with the anteriormost horn having the relatively smaller base. The third horn is short and broad, although not as short as in *P. orbiculare* or *P. douglassi*. *Phrynosoma anzaense* is the only horned lizard examined that has an accessory horn ventral to and between the second and the third horns.

Considerable confusion surrounds the number of horns on the posterior parietal margin among *Phrynosoma* species. In all species of *Phrynosoma*, the posterior border of the parietal is elaborately sculptured with large horns. It can safely be determined that the pattern of two large posterodorsally directed horns is the modal condition; however, in *P. solare*, *P. modestum*, and large *P. douglassi* four parietal horns may be present. But only in *P. solare* is the additional pair of horns significantly developed. A single small median horn that lies between the large horns is present in some species. This horn originates on a bony "osteoderm" along the parietal border and is large in *P. coronatum*, *P. cornutum*, and *P. orbiculare*. This condition may appear as a small oblique horn in some *P. mcalli* and *P. platyrhinos* and is present in the type specimen of *P. anzaense*.

A dense pattern of "osteoderms" covers the en-

tire parietal table. These "osteoderms" are not the true osteoderms formed by intermembrane bone found in some other lizards (e.g. helodermatids, anguines, and varanids), but simply the bony origin of the cranial scalation (Etheridge, pers. comm.). For want of a better term "osteoderm" is used here. The extremely rugose surface of *P. anzaense* is formed of these "osteoderms." Montanucci, although not polarizing these conditions, indicated that "low tuberosities, and conical spine-like tubercles represent progressively derived conditions" (Montanucci, 1987:8). At the base of the large parietal horn in *P. anzaense* lies a single row of sharply pointed "osteoderms," one of which is large and protruding. This feature is a synapomorphy for a group including *P. modestum*, *P. mcalli*, and *P. platyrhinos* (Montanucci, 1987).

The shape of the parietal and its association with the postorbital and squamosal determine the shape of the supratemporal fenestrae. In *P. anzaense* the suture between the parietal and squamosal lies near the middle of the arching posttemporal bar. Owing to the position of the squamosal-parietal suture, a distinct sculptured squamosal process of the parietal is present. In *P. asio*, *P. cornutum*, and *P. solare* this suture lies at the lateral base of the parietal horn, not lateral to an accessory horn as in *P. anzaense*.

The distribution of derived character states used by Montanucci (1987) in analyzing the phylogeny of *Phrynosoma* species indicates that *P. anzaense* is the sister-group to *P. mcalli* in a group containing these species and *P. platyrhinos*, *P. solare*, and *P. modestum*. Several alternative phylogenies are equally parsimonious for this clade, although Montanucci preferred the topology of a sister-group relationship between *P. platyrhinos* and *P. modestum* with *P. mcalli* and *P. solare* as sequential sister-groups.

Species of the genus *Phrynosoma* are poorly known from the early and middle Neogene of North America, only becoming common in Late Pleistocene cave deposits. The earliest occurrence of a *Phrynosoma* species is in the Late Miocene Valentin Formation of Nebraska (Estes and Tihen, 1964). This dentary lacking sculpture or horns is not referred to a species. By the Late Pleistocene specimens referable to extant taxa are present (Brattstrom, 1953, 1955; Etheridge, 1960; Holman, 1970). Three fossil species have been described from Pliocene and Pleistocene beds: *P. adinognathus* (Rickart, 1976) from the early Pleistocene of Kansas, known only from a pair of dentaries and allied with *P. douglassi* (Van Devender and Eshelman, 1980); *P. holmani* (Eshelman, 1975) from the Late Pliocene of Kansas, originally described as a *Sceloporus*; and *P. josecitensis* (Brattstrom, 1955) from the Pleistocene of Nuevo Leon, Mexico, consisting of a skull fragment with four temporal spines and of unknown affinities. All fossil remains are found within the western United States and northern Mexican range of the genus.

Recent *Phrynosoma* species occupy a wide range of habitats, from the mesic yellow-pine forest to desert grassland species *P. douglassi* to the xeric *P. platyrhinos*, making any paleoecologic comparison tenuous. Recent *Phrynosoma* species are diurnal and insectivorous; fecal material and stomach contents show a diet that is almost entirely of ants (Stebbins, 1954). *Phrynosoma mcalli* and *P. platyrhinos* occur as extant species at or near the fossil locality.

Phrynosoma sp.

REFERRED SPECIMEN. LACM 6604/78293, a badly weathered cranium.

DESCRIPTION. Anteriorly both maxillae and prefrontal and nasal fragments are preserved. Portions of the jugal and postorbital delineate an oval orbit. Part of the right squamosal is the only temporal element present. The bone is severely weathered and pitted.

DISCUSSION. The specimen is referred to *Phrynosoma* species indeterminate on the basis of the distinctive peg-like dentition. The very fragmentary nature of the material (such as the lack of a temporal region) preclude lower level comparisons. The only character of note is that LACM 78293 shares with *P. modestum*, *P. mcalli*, *P. platyrhinos*, and *P. solare*, *P. taurus*, *P. cornutum*, and *P. braconieri* the derived character of a prefrontal that borders the external nares separating the maxilla and the nasals.

Sceloporine Type A

Figure 12D

REFERRED SPECIMENS. LACM 6583/78235, 6540/78305, 6540/78306, 6540/78307, 1454/ (unnumbered specimen), 1196/78211, 1196/78212, 6712/20981, 1615/4401, 1615/78721, 1615/78276, 1615/78272, 1113/123323, 1114/78205, 1114/123320, 1114/123321, 1114/123322, 1114/123334, 1114/123333, 6707/78241, 1297/64126; dentary and maxillae fragments.

DESCRIPTION. Sceloporine Type A is a large sceloporine with low-crowned teeth and long columnar tooth shafts. The tooth crowns are tricuspid with a central median cusp and oblique lateral cusps. The central median cusp is bulbous, its outline continuing onto the tooth shaft.

The best specimen, LACM 123320 (Fig. 12D), is a left mid-dentary fragment with eight teeth in 15 tooth spaces. Meckel's groove is closed, but unfused anterior to the Meckelian reentrant. Anteriorly, Meckel's groove flares open. The labial surface of the dentary is smooth with two mental foramina. The teeth are low crowned, reaching less than one-fourth their height above the dental parapet.

The tooth shafts are long, columnar, and curved with resorption pits present at the bases of teeth three, five, and seven; nutrient foramina occupy the

remaining tooth bases. The tooth crowns are tricuspid, however, most of the teeth are worn, giving them an oblique appearance. The central bulbous cusp is flanked by small lateral cusps. The tooth crowns are lingually concave and have striated enamel. The anterior teeth are smaller than those posterior in the jaw.

The remaining materials are fragments of dentaries and maxillae referred to sceloporine Type A on the basis of a similar dental morphology of low-crowned teeth with long columnar shafts and weakly developed tricuspid teeth. A large size range is represented by this material, yet all sizes display similar dental morphology except that the smaller dentaries have teeth with higher crowns, extending approximately one half their height apical to the parapet.

DISCUSSION. Living sceloporines (*sensu* Etheridge and de Queiroz, 1988) form a monophyletic group comprising ten genera and 105 species. Sceloporines can be divided into four generic groups: a *Petrosaurus* Boulenger, 1885, group, a *Urosaurus* Hallowell, 1854–*Sceloporus* Wiegman, 1828–*Sator* Dickerson, 1919–*Uta* Baird and Girard, 1852, group (the sceloporus group of Etheridge and de Queiroz), a *Phrynosoma* group, and a sand lizard group containing *Callisaurus* Blainville, 1835, *Uma* Baird, 1859, *Cophosaurus* Troschel, 1850, and *Holbrookia*. Most of these taxa inhabit south western North America. Etheridge (1964b) described the generic morphologies of the sceloporines and proposed a phylogeny for this informal grouping that has been improved by Etheridge and de Queiroz's (1988) cladistic treatment of these groups' relationships.

In sceloporine Type A, the teeth are low crowned with small lateral cusps. In extant sceloporines, the tooth form within most genera is regular. The most aberrant pattern is seen in *Callisaurus*, which have pointed, blade-like, and unicuspid teeth. Other sand lizards show a more typical iguanid pattern of high-crowned tricuspid teeth. In species of *Holbrookia* and *Cophosaurus* the tooth columns are cone-shaped with expanded bases and small lateral cusps that may be separated from the median cusp by shallow "V"s if the teeth are unworn. In *Uma* spp., the teeth are also very high crowned, have expanded bases, and are more tricuspid than in other sand lizards with lateral cusps widely separated from the median cusp.

The two species of *Petrosaurus* form the sister-group of other sceloporines (Etheridge, 1964b). The teeth are tricuspid with wide laterally expanded crowns and flaring cusps in *P. thalissinus* (Cope, 1863), or tall, slender, and widely spaced, with less flaring cusps in *P. mearnsi* Van Denburgh, 1895. Both species have widened tooth bases. The members of the *Phrynosoma* group are highly distinctive in their small, occasionally tricuspid, cylindrical peg-like teeth.

The *Uta*–*Urosaurus*–*Sator*–*Sceloporus* group has a variable tooth morphology. In *Uta* sp., the teeth are high crowned with expanded cylindrical bases.

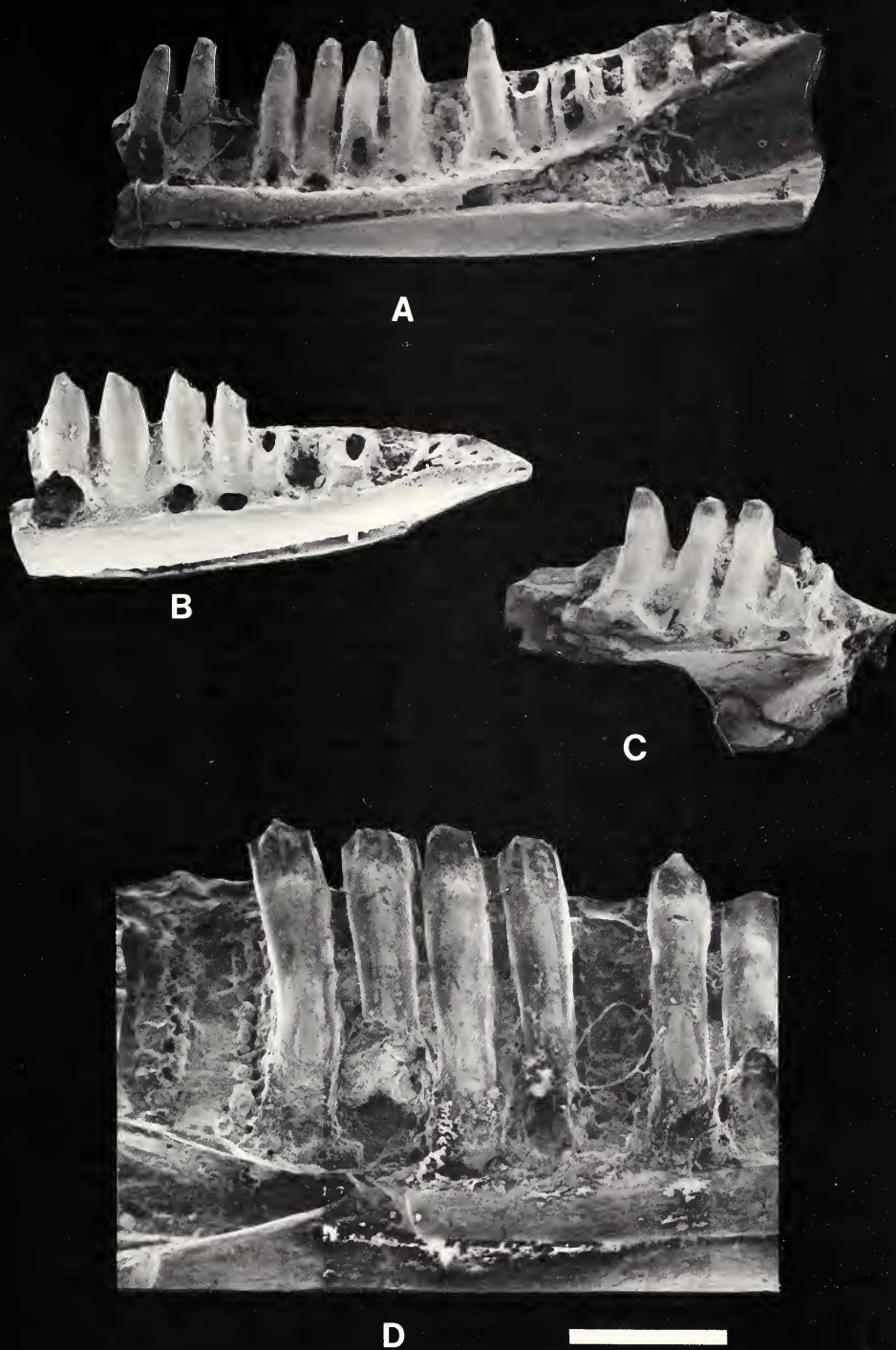


Figure 12. A, sceloporine species B (LACM 1114/123330); B, basal Teiini (LACM 1114/123326); C, *Eumeces* sp. (LACM 1615/78308); and D, sceloporine species A (LACM 1113/123323). Bar = 1 mm.

The unerupted teeth are tricuspid with a large, central median cusp. In worn teeth, the ventral cusp is blunt and the lateral cusps form small shoulders unseparated from the central cusp. *Urosaurus* spp. are small *Uta*-sized lizards with dental morphology that is indistinguishable from some small *Sceloporus* species or *Uta* sp.

Sator sp. has strongly tricuspid teeth with columnar bases. The tooth crowns are laterally compressed. The lateral cusps are separated from the main cusp by shallow "V"s that continue onto the crown surface.

The genus *Sceloporus* is large (70 species) and morphologically diverse (Smith, 1939). Typical *Sceloporus* species have low-crowned, columnar, tricuspid teeth, although much variation is seen in this pattern. In many large *Sceloporus* species, as well as sceloporine Type A, the tooth crowns are curved, giving them a dorsally concave appearance. This modification, as well as crown height, is enhanced during ontogeny with overall deepening of the dentary.

The assignment of these specimens to any taxon within the sceloporine group (except for those taxa that can be eliminated) cannot be defended until a better understanding of the hierarchic distribution of sceloporine characters is achieved. Even with such information, the level of morphologic resolution of such material may never allow such determinations. For instance, Wellstead (1982) and Larsen and Tanner (1974) found no consistent means of distinguishing taxa on the basis of jaw morphology. The Anza Borrego specimens are considered as identifiable morphotypes within the sceloporine group until more detailed information is developed.

Sceloporine Type B

Figure 12A

REFERRED SPECIMENS. LACM 6583/78246, 6583/78247, 6583/78248, 6583/78249, 6583/78250, 1615/4401, 1114/123330, 1114/123331, 1114/123332; fragmentary dentaries; unnumbered specimens possibly referable to sceloporine Type B are found at localities 1461, 6683, 1454.

DISCUSSION. Several small *Uta*-sized dentaries with delicate, very high-crowned teeth are designated sceloporine Type B. The better specimens (Fig. 12A) exhibit teeth that extend over half of their height above the dental parapet. The teeth are cone-shaped, tapering toward small tricuspid, laterally compressed crowns. The median tooth cusps are relatively large, bulbous, and pointed. The lateral cusps are small, flat, and separated from the median cusps by small "V"s that extend onto the tooth columns. The expanded tooth bases and tapering tooth columns give the teeth a widely spaced appearance at the crowns. The tooth bases are excavated by small nutrient foramina or resorption pits.

Meckel's groove is unfused and closes anterior

to the extension of the splenial. The lingual surface of the jaw is rounded and the teeth are set in a shallow dental gutter that expands anteriorly.

The labial surface of the jaw is smooth with small mental foramina anteriorly. Posteriorly, a broad fossa is present dorsally and tapers anteriorly on the large better preserved specimens. Overall the dentary is straight, long, and thin.

DISCUSSION. Sceloporine Type B resembles *Uta* sp. in its small size, teeth with wide bases tapering distally, and high-crowned weakly tricuspid teeth. Unfortunately, other small sceloporines also display a similar pattern, and reference of sceloporine Type B to a lower level taxon cannot be justified.

Infraorder Scincomorpha Camp, 1923

Superfamily Lacertoidea Oppel, 1811

Family Teiidae Gray, 1827

Tribe Teiini Gray, 1827

Ameiva Meyer, 1795,
and/or *Cnemidophorus* sp.
Wagler, 1830

Figure 13

REFERRED SPECIMENS. LACM 6831/20929, a nearly complete cranium and mandibles.

DESCRIPTION. The rugose cranial osteoderms and the heavily sculptured mandibles indicate that the individual was an adult. Anteriorly, the rostrum is crushed and the premaxilla, nasals, most of the prefrontals, and the anterior parts of the maxillae and dentaries are missing. Posteriorly the postorbital bars, squamosals, left quadrate, most of the jugals, and the retroarticular process of the dentaries are not preserved.

DISCUSSION. Within the family Teiidae, Vanzolini and Valencia (1965) recognize two tribes. The tribe Teiini contains the genera *Ameiva*, *Cnemidophorus*, *Teius* Merrem, 1820, *Dicrodon* Duméril and Bibron, 1839, and *Kentropyx* Spix, 1825. A second tribe, the Tupinambini, contains the genera *Dracaena* Daudin, 1802, *Crocodilurus* Spix, 1825, *Tupinambis* Daudin, 1802, and *Callopistes* Gravenhorst, 1838. Presch (1974) indicated that within the Teiini, only the genera *Teius*, *Dicrodon*, and *Kentropyx* are monophyletic and that *Dicrodon* shares derived features with *Teius*. Species of *Kentropyx* possess a single derived feature, a concave parietal, but species of *Ameiva* and *Cnemidophorus* do not share any derived features not common to all Teiini. Presch (1970) reported that species of *Ameiva* possess a tongue sheath, although this feature may vary within the genus (Burt, 1931; Vanzolini and Valencia, 1965). Rieppel (1980) reported that differences exist in the temporal musculature between *Ameiva* spp. and other members of the Teiini, but his sample was limited to two species of *Ameiva* and a single species of *Cnemidophorus*.

Species of *Ameiva* and *Cnemidophorus* are mor-

phologically indistinguishable, and these genera are of dubious monophyly. Estes (1963a) suggested that the genera *Ameiva* and *Cnemidophorus* be synonymized under the name *Ameiva* to eliminate confusion. However, because the genus *Ameiva* is still undiagnosable as a monophyletic taxon, this suggestion is not accepted here until further work demonstrates the monophyletic elements of the *Ameiva/Cnemidophorus* species complex.

LACM 20929 is comparable with extant species of the *Ameiva/Cnemidophorus* complex in its weakly bicusate teeth and slightly convex parietal. During growth *Ameiva/Cnemidophorus* species undergo a great deal of ontogenetic change (Estes and Williams, 1984), osteoderms are fused onto the skull roof and extensive dermal sculpture occurs on the mandibles, with the dentary becoming thick, robust, and sculptured, and the teeth losing their blade-like appearance, becoming short and peg-like. These features in the fossil specimen suggest that it was senescent, a stage unrepresented in the sample of comparative material. Until additional comparative material representing corresponding ontogenetic stages becomes available for study, referral of this specimen in any species-level taxon is unsupported. Nevertheless, the fossil does possess some interesting features. The overhang of the parietal into the supratemporal space, forming a small roof, is more developed in the fossil than in any species of extant *Ameiva/Cnemidophorus* studied. In these specimens, the adductor muscles generally attach on the dorsal surface of the parietal. In *Kentropyx* species this condition is more extreme, and the parietal roof extends far into the supratemporal space. In some older individuals of *Ameiva/Cnemidophorus* spp., rudiments of this condition become apparent.

Living Teiini occur predominantly in South America. The genera *Teius*, *Dicrodon*, and *Kentropyx* are confined to the Neotropics. *Ameiva* species (exclusive of *Cnemidophorus*) exist in South America, the Caribbean, and north into Mexico, whereas species of *Cnemidophorus* live in North America southward into southern South America. Two species (*C. tigris* Baird and Girard, 1852, and *C. hyperythrus* Cope, 1863) occur in the area of the fossil deposit today. Species displaying *Ameiva/Cnemidophorus* dental morphologies are common elements of Neogene North American assemblages. However, these specimens may have been overinterpreted (Estes, 1983; Norell, 1986), and the referral of this material to species should be reinterpreted.

Tribe Teiini Gray, 1827

Genus and species indeterminate

Figure 12B

REFERRED SPECIMENS. LACM 6583/78300, 1454/123325, 1615/78299, 1114/123326, 1114/123327, 1114/123328, 1114/123329, 1114/78194; fragmentary maxillary and dentary fragments.

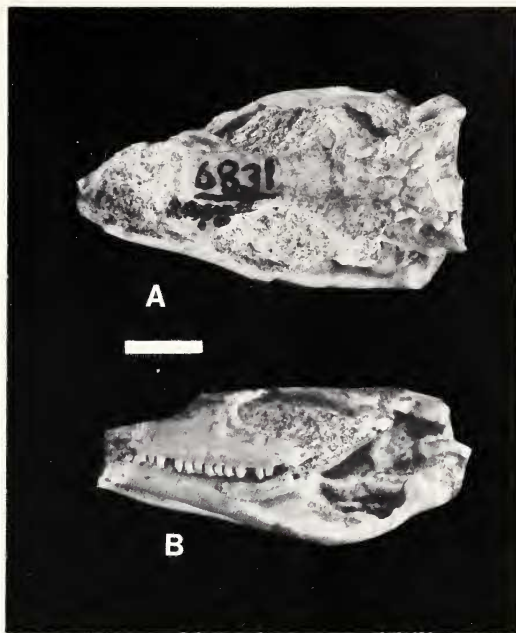


Figure 13. Skull of *Ameiva/Cnemidophorus* LACM 20929 from LACM locality 6831. A, dorsal view; B, left lateral view. Bar = 6 mm.

DISCUSSION. This material is referred to the tribe Teiini on the basis of tooth morphology. These teeth are blade-like and either two- or three-cusped. This tooth morphology is undoubtedly primitive for the Teiidae (Presch, 1974) and is present in *Kentropyx*, *Ameiva*, and *Cnemidophorus*.

Superfamily Scincoidea Oppel, 1811

Family Scincidae Oppel, 1811

Subfamily Scincinae Oppel, 1811

Eumeces Wiegmann, 1834

Eumeces sp.

Figure 12C

REFERRED SPECIMENS. LACM 6522/123324, 1437/78277, 1437/178236, 1615/78308; fragmentary dentaries and maxillae.

DESCRIPTION. The most nearly complete specimen, LACM 78308 (Fig. 12C), is a small (2.2 mm) maxillary fragment containing four teeth. The labial surface of the maxilla is smooth and contains four supralabial foramina, two of which are incomplete. Lingually, five tooth positions are present on a dental shelf. The teeth are low crowned, only projecting 0.37 mm above the maxillary parapet. The tooth columns curve labially from crown to base. Small nutrient foramina are present at the expanded base of each tooth. The tooth crowns are of approximately equal height and width. The striated, lingually concave crowns are canted trans-

versally. The three anterior teeth are worn and separated by equal interdental spaces. The apex of the posterior tooth is relatively more pointed, perhaps indicating that it was newly erupted.

DISCUSSION. Species of *Eumeces* form a primitive, inadequately diagnosed, probably paraphyletic genus of the subfamily Scincinae (Estes, 1983; Greer, 1970). Extant species are found in North America, southwestern Asia, northern Africa, China, and Japan (Greer, 1970). All of the fossil material is confined to North America, with the exception of a Middle Miocene species from Morocco (Rage, 1976). The earliest occurrence of the genus comes from the Early Miocene Thomas Farm locality of Florida (Estes, 1963a).

Specimens are referred to the genus *Eumeces* on comparable tooth morphology and interdental spacing (Estes, 1963a). *Eumeces* species have unicuspid, slightly bulbous, pleurodont teeth, with lingually concave surfaces below obtuse apices. Small ridges on the lingual tooth surfaces form the blunt apices. The concave lingual surface of each tooth is covered by fine enamel striations that terminate abruptly at the base of the crown.

Aside from the problems of referring the fossils to *Eumeces*, the fragmentary nature of the material makes specific assignment difficult. *Eumeces skiltonianus* Baird and Girard, 1852, most closely resembles the fossil specimens in general dental similarity. Two skinks occupy the immediate and surrounding area today: *E. gilberti* Van Denburgh, 1896, and *E. skiltonianus*. *Eumeces gilberti* is a large species, and adults are easily distinguished from the fossil material by their low crowned bulbous teeth with blunt apices. Relative size, general morphologic similarity, and geographic affinity are, however, not sufficient criteria to allow specific identification.

Superfamily Cordyloidea

Fitzinger, 1826

Family Xantusiidae Baird, 1858

Xantusia Baird, 1858

*Xantusia downsi** new metaspecies

Figure 14

DIAGNOSIS. A small xantusiid (tooth row length = 2.87 mm), referred to the genus *Xantusia* (*sensu* Savage, 1963) on the basis of the synapomorphic reduction of tricuspid teeth and a smaller size. *Xantusia downsi** can be distinguished from other species of *Xantusia* by the plesiomorphic presence of a dental gutter. All distinguishing characters of the type species *Xantusia downsi** are plesiomorphic for the genus *Xantusia*.

HOLOTYPE. LACM 1114/123301, a right spleniodentary.

REFERRED SPECIMENS. LACM 1114/78198, 1114/123302, 1114/123303, 1114/123304, 1114/123305, 1114/123306, 1114/123307, 1114/

123308, 1114/123309, 1114/123310, 1114/123311, 1114/123312, 1114/123313, 1114/123315, 1114/123316, 1114/123317, 1114/123318, 1114/123319, 1114/123335, 1323/78292, 6583/78244, 1615/78274; spleniodentary, maxillae, and frontal fragments.

ETYMOLOGY. Named in honor of Theodore Downs for his contribution to our knowledge of Anza Borrego paleontology.

DESCRIPTION OF THE HOLOTYPE. Meckel's groove is closed and fused, opening anteriorly at the mandibular symphysis. A large coronoid process curves posterodorsally and is broken above the level of the tooth crowns. A weak coronoid incision lies lingual to the surface of the coronoid process. Posterolabially, the spleniodentary is broken. A coronoid notch reaches the posteroventral edge of the subdental shelf and borders the anterior mylohyoid and inferior alveolar foramina. A deep subdental gutter forms the dorsal surface of a heavy ventral ridge. Thirteen tooth positions are closely spaced. The first, second, and fifth teeth are missing. The teeth are of equal height and rise approximately one-half of their height above the dental parapet, above which the tooth columns taper to bluntly conical, laterally compressed apices. The tooth enamel is smooth, and the anterior teeth are slightly more pointed and blade-like than the posterior ones. Teeth seven and twelve are excavated at their bases by resorption pits while the bases of the remaining teeth contain nutrient foramina. The labial surface of the dentary is robust and convex. Mental foramina are present below the fifth, seventh, tenth, and twelfth teeth. Posterolabially a smooth, saddle-like fossa lies ventral to the dorsal ridge between the coronoid process and the last tooth.

DESCRIPTION OF REFERRED SPECIMENS.

The referred material indicates that several characters found on the holotype specimen are variable within the taxon. The dental gutter is not as well developed in some of the specimens; nevertheless, it is always more developed than in any *Xantusia* spp. examined. The specimens with a small dental gutter are smaller and not as robust as the holotype specimen.

The splenial depression seen in some species of "*Paleoxantusia*" Hecht, 1956 (Schatzinger, 1980) occurs variably in *X. downsi**. This depression demarks the boundary of the splenial (Gauthier, pers. comm.). A few specimens (LACM 123319 and 123307) have depressions in the region of the inferior alveolar and anterior mylohyoid foramina, whereas similar sized specimens lack this feature.

Maxillae are referred to *X. downsi** on the basis of dental morphology, size, and occurrence at the same locality (LACM 1114). All of the maxillae are fragmentary; the best specimen (LACM 123316) contains nine conical teeth, identical to those in the holotype spleniodentary.

Four frontals from LACM locality 1114 have been provisionally assigned to *X. downsi** because they are xantusiid-like and occur in the same lo-

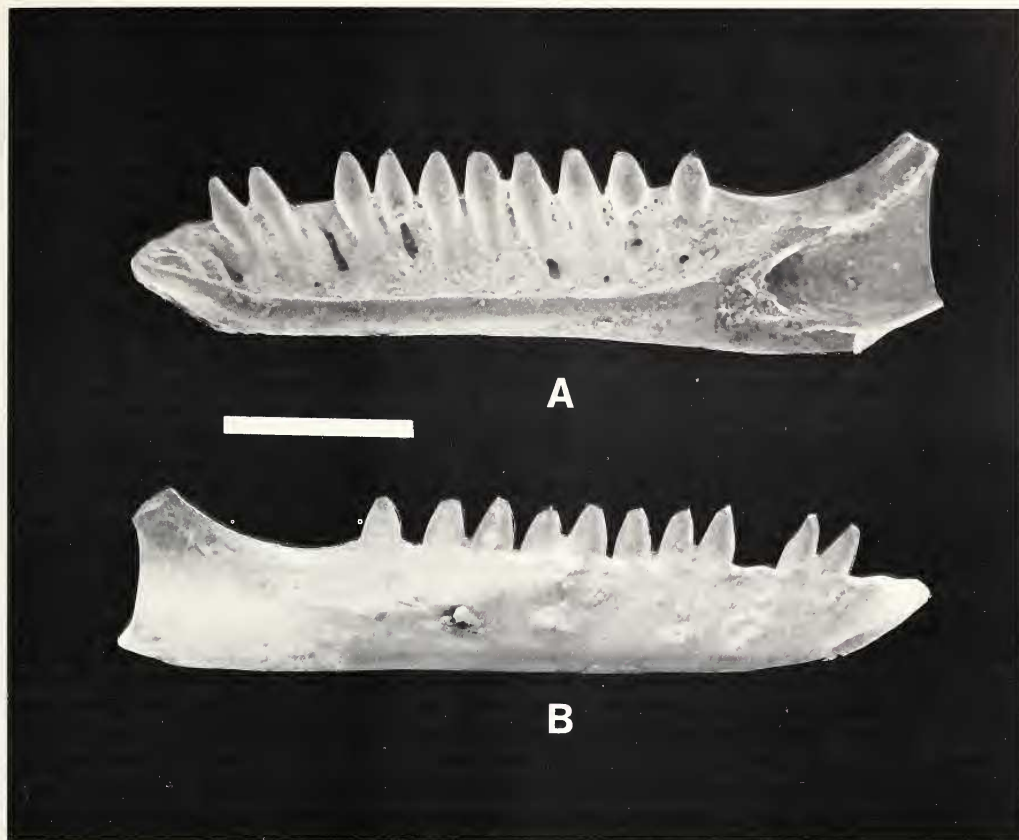


Figure 14. Holotype spleniodentary of *Xantusia downsi** n. metasp., LACM 123301 from LACM locality 1114. A, lingual view of left spleniodentary; B, labial view of left spleniodentary. Bar = 1 mm.

cality with the type dentary material. The frontals resemble *X. vigilis* Baird, 1859, in size and shape, being small and paired with an anterior descending process; however, they are slightly larger than in *X. vigilis*.

DISCUSSION. Living xantusiids constitute three (Bezy and Sites, 1987) or four (Crother *et al.*, 1986) monophyletic generic groups; another group, the fossil genus "*Paleoxantusia*," is "paraphyletic as presently constituted" (Estes, 1983:125).

Contemporary phylogenetic treatments of xantusiids are difficult to apply to the Anza Borrego fossil material because few characters are preserved in these specimens. Here, *Xantusia downsi** is placed as the probable sister-taxon of *Xantusia* on the basis of reduction of the tricuspid teeth, small size, and more delicate dentary compared with members of the "*Paleoxantusia*" grade and other xantusiids.

The tooth form of living species of *Xantusia sensu* Savage (1963) and Crother *et al.* (1986) (including only *X. vigilis* and *X. henshawi*) is usually conical with blunt posterior teeth grading into sharper anterior teeth. In some individuals, minute lateral cusps are present on teeth near the middle of the tooth row. The teeth are often slightly laterally compressed and show a slight lingual con-

cavity. Small enamel striations are present near the bases of the tooth crowns. The condition in *X. downsi** is similar, except that the teeth are more robust and begin to taper toward the apices at the level of the dentary parapet rather than dorsally and lack striations on the tooth crown bases.

*Xantusia downsi** is not referable to species of the extant taxa *Lepidophyma* Duméril, 1851, *Cricosaura typica* Gundlach and Peters, 1863, or *Klauberina riversiana* (Cope, 1883) on the basis of dental morphology and tooth number. In *K. riversiana* the teeth are trifid, with flaring lateral cusps placed in a single line (Hecht, 1956; *contra* Crother *et al.*, 1986). *Lepidophyma* species have posterior teeth with a unique pattern of lateral cusps rotated lingually, forming a superficially tribosphenic molar-like crown. The teeth of *Cricosaura typica* are low crowned with blunt apices. Species of "*Paleoxantusia*" show highly variable tooth patterns. In *P. borealis* Holman, 1972, the teeth have minute lateral cusps. "*Paleoxantusia*" *fera* Hecht, 1956, and *P. allisoni* Schatzinger, 1980, show diminutive lateral cusps while in *P. kyrentos* Schatzinger, 1980, the teeth are distinctly trifid but without flaring lateral cusps and the posterior teeth are somewhat molariform.

A smooth groove on the labial surface of the

coronoid process for insertion of the adductor musculature is present in some xantusiids and is variably present in *X. downsi**. The holotype exhibits a smooth coronoid process, however, LACM 123305 as well as other specimens have smooth, furrow-like grooves, just ventral to the dorsal edge of the coronoid process, that extend posteriorly. Specimens with this condition are smaller and more delicate than those with a smooth coronoid process.

No extant *Xantusia* species studied displays the distinct subdental gutter seen in *X. downsi**. This feature, which occurs in some "*Paleoxantusia*" and other xantusiids, is primitive for the genus *Xantusia*. The dentary is also more robust and deeper in *X. downsi** than in *X. vigilis* or *X. henshawi*. *Xantusia henshawi* has a long, thin dentary quite distinct from all other xantusiids. The dentaries of *X. vigilis* and *X. downsi** are short, however, the dentary of *X. downsi** is more heavily constructed and more like "*Paleoxantusia*" (especially "*P.*" *fera*) than *X. vigilis*. Measurements taken of the labial dentary depth at the penultimate posterior tooth on *X. vigilis* gave a mean depth of 0.69 mm (20 specimens measured) compared to 0.79 mm for *X. downsi**. These values are statistically different.

Although there is some overlap in the morphologies of *X. downsi** and *X. vigilis*, almost all of the Anza Borrego specimens are readily distinguished from other *Xantusia* species. The most recent phylogenetic treatment of the Xantusiidae failed to support a single phylogenetic hypothesis on morphologic grounds (Crother *et al.*, 1986). One hypothesis was, however, congruent with an hypothesis based on chromosomal information (Bezy, 1972) that suggested a sister-group relationship between *K. riversiana* and species of *Xantusia*. However, further work by Bezy and Sites (1987) on allozyme data indicated that *Klauberina* may be derived from within *Xantusia*.

The two extant species of *Xantusia* are diagnosable and may form a monophyletic group exclusive of other Xantusiidae (Crother *et al.*, 1986). Provisionally, I consider *X. downsi** to be their sister-group, lacking the derived features of a thin, lightly constructed jaw, and the loss of the dental gutter. *Xantusia downsi** is designated a metataxon because no diagnostic unequivocally derived features were discovered. It is tempting to consider *X. downsi** as representative of a new genus that is the sister-taxon to *Xantusia*. However, because the monophyly of *Xantusia* has been questioned by Bezy and Sites (1987) this suggestion is dependent on further phylogenetic analysis of this group.

Xantusiids are poorly known in Neogene deposits, however, unstudied *Xantusia*-like forms are present in the Late Miocene age Ricardo Formation, the Middle Miocene Barstow Formation (Gauthier, pers. comm.), as well as at Late Pleistocene localities along the Mojave River, San Bernardino County, California. Whistler (1984) reported on an additional Early Middle Miocene specimen of possible "*Paleoxantusia*" grade from

the Boron Local Fauna of southern California. This specimen is, however, unreferrable to *Xantusia* on the basis of derived characters. Pleistocene specimens referred to the genus *Xantusia* (Brattstrom, 1953) from Rancho La Brea are apparently iguanids (Estes, 1983).

Living species of *Xantusia* are small, secretive, nocturnal or crepuscular lizards that are either saxicolous or live under decomposing yucca and agave. Both *X. vigilis* and *X. henshawi* inhabit the general region of the Anza Borrego deposit today.

Infraorder Anguinomorpha Furbringer, 1900

Superfamily Anguioidea Gray, 1825

Family Anguidae Gray, 1825

Subfamily Gerrhonotinae Tihen, 1949

Genus and species undetermined

Figure 15

REFERRED SPECIMENS. LACM 6552/10601; cranium and mandibles.

DESCRIPTION. The skull is laterally deformed and weathered on the right anterolateral side; most of the right side of the basicranium and the temporal regions are fragmentary. Overpreparation prior to my study of the specimen fragmented most of the cranial osteoderms and destroyed all teeth in the left maxilla.

DISCUSSION. The specimen is referable to the anguid subgroup Gerrhonotinae on the basis of the presence of an anterior process of the surangular, a fused surangular, prearticular, and articular, long anterior and posterior maxillary processes, and the presence of the derived conditions of a fused frontal that is constricted above the orbits, long thin supratemporals and frontoparietal scales in contact on the midline (Estes, 1983; as modified from Mesozoely, 1970, Gauthier, 1982, and Good, 1987).

A specific or generic assignment of the Anza Borrego gerrhonotine is difficult to defend with character information. Until recently, no comparative treatment of the osteology of the extant gerrhonotines has been undertaken. Good's (1987, 1988) review of gerrhonotine osteology and phylogeny is difficult to apply to the Anza Borrego specimen, because most of the features considered in this work are not preserved or difficult to interpret in the Anza Borrego fossil. Furthermore, the gerrhonotine group is speciose and poorly represented in osteologic collections, disallowing detailed comparison of species at this time.

Of the 96 characters Good (1987) used in establishing relationships within the Gerrhonotinae, only a few can be directly examined. The following discussion is based on Good's work and polarities of characters were extracted from his analysis.

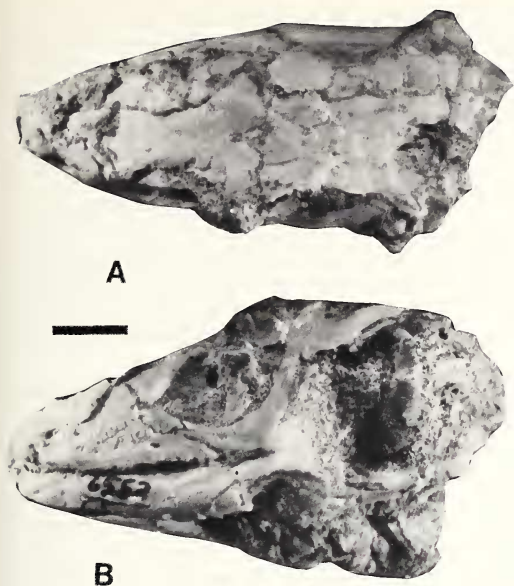


Figure 15. Unidentified fossil gerrhonotine, LACM 10601 from LACM locality 65116. A, dorsal view; B, left lateral view. Bar = 4 mm.

The specimen displays a number of features primitive for the entire gerrhonotine group, including a narrow premaxillary process, a maxilla that does not extend markedly posterior to the ultimate tooth, an unexpanded cephalic condyle of the quadrate, a lacrimal furrow lying at the lacrimal-prefrontal suture, an elongate surangular, a parietal that is visible in lateral view (although this may be an artifact of crushing), and a labial dentary surface lacking a subdental groove.

Derived characters that can be observed on this specimen are few and difficult to interpret. Nevertheless these characters may indicate relationship with a subgroup of gerrhonotines. The Anza Borrego specimen shares with all gerrhonotines, except *Gerrhonotus* Wiegman, 1828, species, a maxilla-prefrontal suture that is not straight; whether the condition in the fossil specimen is like that in species of *Abronia* Gray, 1838 (a "W"-shaped suture), cannot be determined. The fossil specimen also shares a label expansion of the posterior dorsal surangular with this group.

A few features suggest a special relationship with species of *Abronia*. These features include the shared derived presence of a supralabial groove on the maxilla dorsal to the posterior teeth and the reduction of the lateral concave surface of the quadrate. In addition to these characters, the fossil specimen exhibits the derived presence of a lacrimal and jugal everted at the maxillary suture. Relationship with *Abronia* is contradicted by the lack of a posterior groove on the dentary ventral to the tooth row, a derived feature found in species of *Abronia* and its immediate sister-groups but lacking in LACM 10601.

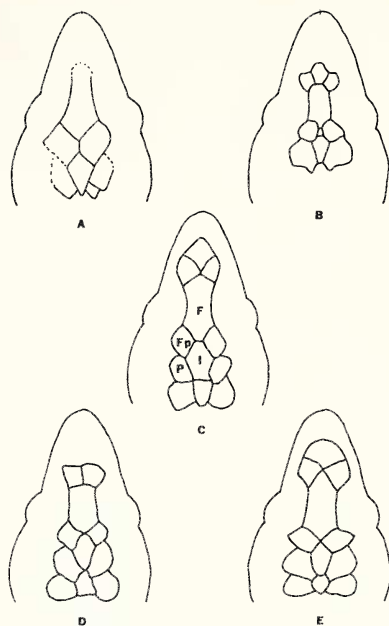


Figure 16. Cranial osteoderms of gerrhonotines. A, LACM 10601, B, *Abronia ornelasi* (modified from Campbell, 1984), C, *Gerrhonotus liocephalus infernalis*, D, *Barisia imbricata*, and E, *Elgaria coerulea*. (C-E modified from Waddick and Smith, 1974). F, frontoparietal; Pa, parietal; Fp, frontoparietal; Ip, interparietal.

Assessing the relationships of this specimen within the phylogenetic system proposed by Good is difficult, because so few features are well enough preserved to allow detailed comparison. Similar difficulties lead Good (1988) to remove all but two of 166 previously referred specimens from the gerrhonotinae. Although LACM 10601 is well preserved, by fossil standards, its relationships are still unclear.

In addition to the cranial characteristics listed above, the pattern of cephalic osteoderms found in the Anza Borrego specimen is unique among gerrhonotines examined during this study. *Abronia taeniata* (Wiegmann, 1834) has large, heavily sculptured cranial osteoderms, unlike the fine sculpturing seen on other gerrhonotines, except for the moderately sculptured *Barisia imbricata* (Wiegmann, 1834)/*gadovi* (Boulenger, 1913) group and the fossil *P. ricardoensis*. Unique to *P. ricardoensis* is a pattern of osteosclerites on the frontal in which a single anterior osteosclerite is bordered posteriorly by a relatively high number of irregularly shaped osteosclerites (Estes, 1963b), a pattern present in LACM 10601. The frontal scute pattern of the Anza Borrego specimen is unusual in the broad contact between the frontoparietal scutes at the midline. The characteristic gerrhonotine frontal pattern appears to be a single, large anterior frontal scute and a pair of frontoparietal scutes partially separated by the anterior portion of the interparietal scute (Fig. 16). In *A. taeniata* the frontoparietal scutes are

narrowly separated by a posterior projection of the frontal scute. The Anza Borrego specimen has two frontoparietal scutes in contact along the midline anterior to the terminus of the interparietal scute. However, this morphology may be subject to variation (Estes, pers. comm.), limiting its phylogenetic efficacy.

Gerrhonotines form a natural group of morphologically and behaviorally diverse forms. *Abronia* spp. are specialized arboreal and generalized forms, while *Elgaria* Gray, 1838, and *Gerrhonotus* are composed of generalized species with large ranges. The species *Elgaria multicarinata* Fitch, 1934, occupies the general region of the locality today. Although fossils from as far back as the Late Cretaceous (Armstrong-Ziegler, 1978) have been referred to the Gerrhonotinae, Good (1988) indicates that these determinations were premature. The earliest occurring taxon that shares apomorphy with a gerrhonotine subclade is *Paragerrhonotus ricardensis*. This specimen is a member of the gerrhonotine crown group and, therefore, is part of the Gerrhonotinae *sensu stricto*, even to the point that Good (1988) noted this taxon should perhaps be synonymized with *Abronia*. It is interesting that this additional regional occurrence of a fossil gerrhonotine shows affinities with the gerrhonotine crown group; Recent members of this clade are native to central Mexico. The putative presence of these related taxa in the Late Tertiary of southern California suggests that the distribution of this group was once more widespread.

PALEOECOLOGY

The climate of the Anza Borrego region changed dramatically during the period of time represented by the Palm Springs Formation. During the Neogene, North American climate had deteriorated from warm subtropical and tropical in the Late Miocene and Early Pliocene to cold and arid in the Late Pleistocene (Hibbard, 1960). Deposition of the Palm Springs Formation occurred during the Early and Late Pliocene and Early Pleistocene epochs, correlative with the Blancan and Early Irvingtonian land mammal ages.

Evidence from a deep-well core at Searles Lake, California (Liddicoat *et al.*, 1980) suggests that the Nebraskan glacial stage, occurring near the middle of the Vallecito Creek local faunal zone, signified the onset of more mesic or pluvial conditions in the region, approximately 1.8 ma. Although the area of the deposit was never glaciated, regional glacial conditions near Mammoth Lakes (Inyo County, California), signified by the Deadman Pass Glacial Till (Currey, 1966), may indicate a general cooling trend in local conditions beginning 3.1 ma.

Following the onset of the initial Nebraskan continental glaciation, glacial activity culminated, receding at the beginning of the Aftonian interglacial, which corresponded with the top of the Palm Springs Formation. The effect of the large scale glaciation

in periglacial areas has been debated. Conditions during glacial maxima are thought to have been more mesic than during periods of glacial retreat (Auffenberg and Milstead, 1969). Experimental modeling evidence contradicts this reasoning, as wet conditions are correlated with general glacial retreat and aridity with glacial advance (West, 1977). The close proximity of large Sierra Nevadan ice sheets may have brought runoff into the Colorado River drainage. The Palm Springs Formation is intercalated with oyster beds (Downs and Woodard, 1961), and tectonic evidence caused Johnson *et al.* (1983) to suggest that deposition of the entire section occurred at or near sea level.

Lizard producing localities from Anza Borrego extend through 2500 m of section representing approximately two million years of deposition. Considering the probable climatic change during the Late Pliocene and Early Pleistocene in the Anza Borrego desert and the large scale temporal mammalian faunal replacements (Downs and White, 1968), changes in lizard community composition would not be surprising.

Figure 17 indicates the stratigraphic occurrence of lizard fossils in the Palm Springs Formation. Taxonomic composition of the assemblage changes temporally. Most obvious is the disappearance of the iguanine genera *D. dorsalis* and *P. novaceki** at approximately zone 40, near the middle of the Arroyo Seco local faunal zone. The subsequent appearance of several more mesic taxa (such as the gerrhonotine and the skink) after the disappearance of all iguanine genera may be an indicator of regional extinction followed by replacement. Argument for environmental change is strengthened (albeit untestable) by comparison with the stratigraphic distribution of the mammalian taxa. Near zone 40, a discontinuity in taxonomic composition, signified by several first and last appearances, caused Downs and White (1968) to place the boundary between the Arroyo Seco and Vallecito Creek local faunas at approximately zone 45.

However, sampling factors may bear on the apparent temporal pattern of lizard fossil occurrence. Fossil materials in the lower part of the section (Layer Cake and lower Arroyo Seco local faunal zone) are large, nearly complete specimens (primarily skulls), collected by traditional paleontologic methods of surface prospecting. More dense concentrations of bone, higher in the section, allowed some localities to be screen washed. Screen washing produced several taxa of small lizards that are not represented in the lower part of the section.

This sampling bias may explain the absence of many taxa low in the section but does not account for the absence of Arroyo Seco local fauna taxa in the Vallecito Creek local fauna. The apparent extinction of two large, phylogenetically allied, herbivorous taxa correlates with the regional first occurrence of several mammalian taxa that suggest a spread of grassland and savanna habitat (Becker and White, 1981). The apparent earlier faunal discon-

tinuity (zone 40 as opposed to zone 46) in lizards relative to mammals is probably also a sampling artifact because lizards are not as common as mammals or found at as many localities. This pattern may characterize a regional change in floral composition reflecting climatic effects.

COMPARISON OF FAUNA

The Anza Borrego assemblage is the most diverse Neogene lizard assemblage yet collected (Table 1), but it shares only minimal taxonomic similarity with temporally bracketing assemblages. Problems with this comparison are two-fold. The limit of morphologic resolution provided by many lizard fossils is at the subfamilial level or above. Considering that most of these higher level taxa have temporal ranges extending through most of the Neogene, such comparisons are of little value. Second, late Tertiary lizard assemblages are taxonomically depauperate with only a few specimens representing a small number of taxa. A characteristic late Tertiary assemblage from western North America includes a *Eumeces*-like skink, one or two sceloporines, iguanids, and an *Elgaria*-like gerrhonotine, limiting the range of possible taxonomic comparisons.

In the immediate vicinity of the Anza Borrego region are several bracketing fossil assemblages. Approximately 100 km north of the Anza Borrego are the outcrops of the Barstow Formation (Barstovian), which has produced a few fossil lizard taxa (Lindsay, 1972). Aside from the typical Neogene lizards, the Barstow Formation has produced an unnamed xantusiid similar to *X. downsi** (Gauthier, pers. comm.). This same xantusiid is also present in the younger Dove Springs Formation (Clarendonian), in conjunction with the monotypic *Paragerrhonotus ricardoensis* (Estes, 1963b) and the typical Neogene assortment of sceloporines, anguids, and skinks (Whistler, pers. comm.).

In the Cajon Formation (San Bernardino County, California; Barstovian-Hemphillian) a small gerrhonotine and some fragmentary sceloporine material have recently been collected (pers. obs.). The Wye local fauna of similar age, in the Crowder Formation of San Bernardino County, California, has also produced a typical Neogene suite of lizard fossils (pers. obs.).

The Tesuque Formation of New Mexico contains a few very interesting unstudied lizard specimens, including a gerrhonotine, a small iguanid of uncertain affinities, and an unnamed iguanine (Norell and de Queiroz, in prep.). The preservation of this material is reminiscent of that from Anza Borrego.

No contemporaneous lizard assemblages exist in the immediate Anza Borrego area. Outside the region, however, several localities from the southern Great Plains produce Blancan land mammals associated with lizard fossils. Beck Ranch (Rogers, 1976) has produced several taxa including a gerrhonotine, three sceloporines, a *Phrynosoma*

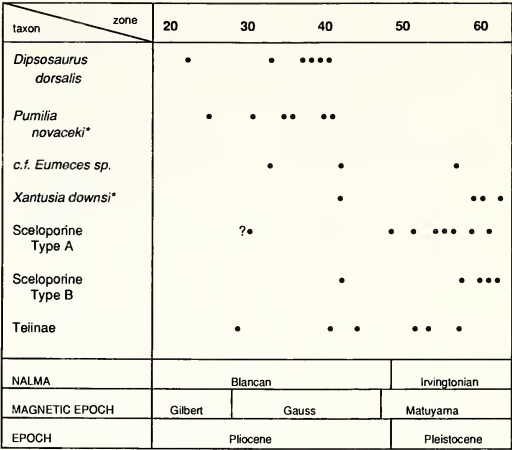


Figure 17. Stratigraphic occurrence of Anza Borrego lizard fossils.

species, two teiid species, and two skink species. Because comparisons in Roger's study were geographically limited, the identifications of these taxa to the species level is dubious. The best known Late Pliocene assemblage from the Great Plains occurs at Rexroad Kansas (Taylor, 1941; Hibbard, 1941). This deposit has produced lizard fossils from several localities, but it shares no specific taxa with the Anza Borrego assemblage.

The Curtis Ranch locality (Lammers, 1970; Harrison, 1972) in southern Arizona is the only temporally equivalent deposit in the region. It has produced numerous, mostly unstudied, lizard fossils, with several modern taxa (pers. obs.).

Taxa from the Anza Borrego Desert are only marginally comparable to specimens from other localities of equivalent age. Not until the Middle or Late Pleistocene do good samples of lizard fossils occur. Unsurprisingly, these show a distinctly modern assortment of taxa. The Anza Borrego fauna shows a high level of endemism that mirrors the condition of the extant lizard fauna. The high endemism may be due more to the remarkable preservation of the Anza Borrego material than to its taxonomic uniqueness. Unlike mammals, lizards typically do not show a wide range of easily recognizable dental characteristics and are poorly represented fossils. Nevertheless the striking similarity of the Anza Borrego fossil assemblage with the Anza Borrego extant fauna is in contrast with the mammalian taxa, for which relatively few extant genera occur in the fossil deposit. This pattern is typical of regional Pleistocene localities (Norell, 1986) and may indicate the relative greater age of lizard genera compared to mammals (Peabody and Savage, 1958).

CONCLUSIONS

Unlike many fossil lizard specimens, the outstanding preservation of the Anza Borrego material al-

lows taxonomic referrals to be made with confidence. The taxonomic analysis indicates that Late Pliocene and Early Pleistocene regional assemblages were dominated by members of the Iguanidae, as is the modern fauna. Many of the fossil genera, including *Dipsosaurus*, *Phrynosoma*, *Gambelia*, cf. *Eumeces*, and *Ameiva-Cnemidophorus*, are ubiquitous lizards in the Anza Borrego region today. Additionally, the metaspecies *Xantusia downsi** is closely related to local *Xantusia* species. The only demonstrably extralimital taxon, in the sense that no close cladistic relatives occur regionally, is the metaspecies *Pumilia novaceki**, which is the sister-taxon of *Iguana*. The northernmost occurrence of the genus *Iguana*, in the riparian gallery forests of western Mexico, coincides with a lizard assemblage that is similar at the generic level to the lizard assemblage described here and may indicate a region of similar habitat to Anza Borrego during Late Pliocene time.

This analysis elucidates the difficulty in assigning specimens to species or genera when cladistic structure and character hierarchies within the groups are unknown or when material has been diagnosed on the basis of characters that are rarely preserved in fossil specimens. Failure to recognize these difficulties has resulted in the identification and allocation of many lizard fossils to taxa on the basis of plesiomorphy or geographic location. Others have simply been overinterpreted. This problem causes the study of regional evolutionary patterns and distributions to be difficult and imprecise. Unless the pattern of taxa through time is portrayed as a hierarchical branching of monophyletic taxa, the data are not applicable to these questions. These problems indicate that a better understanding of the temporal and regional history of lizards will not necessarily require a better fossil record—only a rigorous reinterpretation of the existing one, cast within a framework of living taxa.

The Anza Borrego lizard assemblage is taxonomically the most diverse Neogene assemblage yet documented. The analysis of these specimens indicates that many taxa occupying the area today have a long history in the region, because much of their phylogenetic proliferation was previous to the deposition of the Palm Springs Formation. This agrees with other findings that generic radiation of many of the region's extant genera occurred relatively early and may be associated with the origin of the Madro-Tertiary geoflora in the Early Miocene (Axelrod, 1958; Peabody and Savage, 1958; Savage, 1960, 1967). The early occurrence of many genera and their persistence in the fossil record indicates that the diverse lizard fauna of southwestern North America has developed *in situ*, rather than arisen as the product of recent immigration (*contra* Tihen, 1964).

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LITERATURE CITED

- Armstrong-Ziegler, J. 1978. An aniliid snake and associated vertebrates from the Campanian of New Mexico. *Journal of Paleontology* 52(2):480-483.
- Auffenberg, W., and C. Milstead. 1969. Pleistocene reptiles and amphibians in North America. In *The Quaternary of the United States: a review volume for the VII Congress of the International Association for Quaternary Research*, ed. E. Wright and D. Fry. Princeton: Princeton University Press.
- Avery, D., and W. Tanner. 1971. *Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters*. Science Bulletin, Biological Series, no. 12(3), 79 pp. Brigham Young University.
- Axelrod, D.I. 1958. Evolution of the Madro-Tertiary geoflora. *Botanical Review* 24(7):433-509.
- Baez, A.M., and Z.B. Gasparini. 1977. Orígenes y evolución de los anfibios y reptiles del Cenozoico de América del sur. *Acta Geológica Lilloana* 14:149-232.
- Becker, J., and J.A. White. 1981. Late Cenozoic geomysids (Mammalia: Rodentia) from the Anza-Borrego Desert, Southern California. *Journal of Vertebrate Paleontology* 1(2):211-218.
- Bezy, R.L. 1972. *Karyotypic variation and evolution of the lizards in the family Xantusiidae*. Contributions in Science, no. 227, 29 pp. Natural History Museum of Los Angeles County.
- Bezy, R.L., and J.W. Sites, Jr. 1987. A preliminary study of allozyme evolution in the lizard family Xantusiidae. *Herpetologica* 43(3):280-292.
- Boulenger, G.A. 1890. On the distinctive cranial characters of the iguanoid lizards allied to *Iguana*. *Annals and Magazine of Natural History* 6:412-414.
- Brattstrom, B.H. 1953. The amphibians and reptiles from Rancho La Brea. *Transactions of the San Diego Society of Natural History* 11:365-392.
- . 1955. Pleistocene lizards from San Josecito Cavern Mexico, with description of a new species. *Copeia* 1955:133-134.
- . 1958. New records of Cenozoic amphibians and reptiles from California. *Bulletin of the Southern California Academy of Sciences* 57:5-13.
- . 1961. Some new fossil tortoises from western North America with remarks on the zoogeography and paleontology of tortoises. *Journal of Paleontology* 35:543-574.
- Burt, C. 1931. *A study of the teiid lizards of the genus Cnemidophorus with special reference to their phylogenetic relationships*. Bulletin, no. 154, 286 pp. United States National Museum.
- Campbell, J. 1984. A new species of *Abronia* (Sauria: Anguillidae) with comments on the herpetology of the

- highlands of southern Mexico. *Herpetologica* 40(4): 373-381.
- Crother, B., M. Miyamoto, and W. Presch. 1986. Phylogeny and biogeography of the lizard family Xantusiidae. *Systematic Zoology* 35(1):37-45.
- Currey, R. 1966. Glaciation about 3,000,000 years ago in the Sierra Nevada. *Science* 154:770-771.
- de Queiroz, K.D. 1987. *Phylogenetic systematics of iguanine lizards: a comparative osteological study*. University of California Publications in Zoology.
- De Witt, C.B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana *Dipsosaurus dorsalis*. *Physiological Zoology* 40:49-66.
- Donoghue, M.J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *Bryologist* 88:172-181.
- Downs, T., and J. White. 1968. A vertebrate faunal succession in superposed sediments from Late Pliocene to Middle Pleistocene in California. XXIII International Geological Congress, Vol. 10:41-47.
- Downs, T., and G. Woodard. 1961. Middle Pleistocene extension of the Gulf of California into the Imperial Valley (abs.). Special Paper 68, no. 12, p. 31. Geological Society of America.
- Eshelman, R. 1975. Geology and paleontology of the Early Pleistocene (late Blancan) White Rock fauna from north-central Kansas. *University of Michigan Paleontologic Papers* 13:1-10.
- Estes, R. 1963a. Early Miocene salamanders and lizards from Florida. *Quarterly Journal of the Florida Academy of Science* 26:234-256.
- . 1963b. A new gerrhonotiform lizard from the Pliocene of California. *Copeia* 1963(4):676-680.
- . 1983. *Handbuch der Paleoherpetologie. Part 10A: Sauria Terrestria*. Stuttgart: Gerhard Fischer Verlag.
- Estes, R., and J. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. *American Midland Naturalist* 72:453-472.
- Estes, R., and E. Williams. 1984. Ontogenetic variation in the molariform teeth of lizards. *Journal of Vertebrate Paleontology* 4(1):96-107.
- Etheridge, R. 1958. Pleistocene lizards of the Cragin Quarry fauna of Meade County Kansas. *Copeia* 1958: 94-101.
- . 1960. Additional notes on the lizards of the Cragin Quarry fauna. *Papers of the Michigan Academy of Sciences* 45:113-117.
- . 1964a. Late Pleistocene lizards from Barbuda, British West Indies. *Bulletin of the Florida State Museum* 9(2):43-75.
- . 1964b. The skeletal morphology and systematic relationships of sceloporine lizards. *Copeia* 1964(4): 610-631.
- . 1965. Fossil lizards from the Dominican Republic. *Quarterly Journal of the Florida Academy of Sciences* 28:349-358.
- . 1966. The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus*. *Copeia* 1966:79-91.
- Etheridge, R., and K.D. de Queiroz. 1988. A phylogeny of Iguanidae. In *The phylogenetic relationships of the lizard families*, ed. R. Estes and G. Pregill, pp. 283-368. Palo Alto: Stanford University Press.
- Gaffney, G. 1979. An introduction to the logic of phylogeny reconstruction. In *Phylogenetic analysis and paleontology*, ed. J. Cracraft and N. Eldredge, pp. 79-111. New York: Columbia University Press.
- Gauthier, J.A. 1982. Fossil xenosaurid and anguid lizards from the Early Eocene Wasatch Formation, south-east Wyoming, and a revision of the Anguioidea. *Contributions to Geology*. Univ. Wyoming 21(1):7-54.
- . 1984. A cladistic analysis of the higher systematic categories of the Diapsida. Berkeley: University of California. Dissertation.
- Gauthier, J.A., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. In *Phylogenetic relationships of the lizard families*, ed. R. Estes and G. Pregill, pp. 15-98. Palo Alto: Stanford University Press.
- Good, D.A. 1987. A phylogenetic analysis of cranial osteology in the gerrhonotiform lizards (Squamata: Anguidae). *Copeia* 1987:696-701.
- . 1988. The phylogenetic position of fossils assigned to the Gerrhontinae (Squamata: Anguidae). *Journal of Vertebrate Paleontology* 8(2):188-195.
- Greer, A. 1970. A subfamilial classification of scincid lizards. Bulletin of the Museum of Comparative Zoology, 139(3), pp. 151-184. Harvard University.
- Hallowell, E. 1854. Description of new reptiles from California. *Proceedings of the Academy of Natural Sciences, Philadelphia* 7:91-97.
- Hardy, L.M., and R.W. McDiarmid. 1969. The amphibians and reptiles of Sinaloa, México. *University of Kansas Publications of the Museum of Natural History* 18(3):39-252.
- Harland, W.B., A.V. Cox, P.G. Llewellyn, C.A.G. Pickton, A.G. Smith, and R. Walters. 1982. *A geologic time scale*. Cambridge: Cambridge University. 131 pp.
- Harrison, J. 1972. The mammals of the Wolf local fauna, St. David Formation, Cochise County, Arizona. Tucson: University of Arizona. Dissertation.
- Hecht, M. 1956. A new xantusiid lizard from the Eocene of Wyoming. *Novitates*, no. 1774, 8 pp. American Museum of Natural History.
- Hibbard, C. 1941. Paleogeology and correlation of the Rexroad fauna from the upper Pliocene of southwestern Kansas, as indicated by the mammals. *University of Kansas Science Bulletin* 27(6):79-104.
- . 1960. An interpretation of Pliocene and Pleistocene climates in North America. *Michigan Academy of Science, Arts and Letters (Annual) Report* 62:5-30.
- Hoffstetter, R. 1940. Appendice sur la faune précolombienne de l'anse Belleville, 2: Les Reptiles. *Journal Societe des Americanistes, Nouvelle Series* 32:268-272.
- . 1946. *Faune du gisement précolombienne d'anse Belleville (Martinique): reptiles*. Memoires Nouvelle Series 22, p. 18. Musee de Naturelle Histoire, Paris.
- . 1970. Vertebrados Cenozoicos de Ecuador. *Actas IV Congress de Latinoamerica Zoologica, Caracas* 2:955-970.
- Holman, J.A. 1970. A Pleistocene herpetofauna from Eddy County, New Mexico. *Texas Journal of Science* 22(1):29-39.
- . 1972. Herpetofauna of the Calf Creek local fauna (Lower Oligocene: Cypress Hills Formation) of Saskatchewan. *Canadian Journal of Earth Science* 9:1612-1631.
- Holman, J., and R. Sullivan. 1981. A small herpetofauna from the type section of the Valentine Formation (Miocene: Barstovian), Cherry County, Nebraska. *Journal of Paleontology* 55(1):138-144.
- Howard, H. 1963. *Fossil birds of the Anza-Borrego*

- Desert. Contributions in Science, no. 73, 33 pp. Natural History Museum of Los Angeles County.
- Johnson, N.M., C.B. Officer, N.D. Opdyke, G.D. Woodard, P.K. Zeitler, and E.H. Lindsay. 1983. Rates of Cenozoic tectonism in the Vallecito-Fish Creek basin, western Imperial Valley, California. *Geology* 11:664-667.
- Lammers, G. 1970. The Late Cenozoic Benson and Curtis faunas of the San Pedro Valley Cochise County, Arizona. Tucson: University of Arizona. Dissertation.
- Larsen, K.R., and W.W. Tanner. 1974. Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. *Great Basin Naturalist* 34:1-41.
- Lazell, J. 1973. *The lizard genus Iguana in the Lesser Antilles*. Bulletin of the Museum of Comparative Zoology, no. 145(1), 28 pp. Harvard University.
- Liddicoat, J., N. Opdyke, and G. Smith. 1980. Paleomagnetic polarity in a 930 m core from Searles Valley, California. *Nature* 286:22-25.
- Lindsay, E. 1972. *Small mammal fossils from the Barstow Formation, California*. Publications in Geological Sciences, no. 93, 104 pp. University of California.
- Merriam, R., and O. Bandy. 1965. Source of Upper Cenozoic sediments in the Colorado Delta region. *Journal of Sedimentary Petrology* 35:911-916.
- Meszoely, C. 1970. *North American fossil anigid lizards*. Bulletin of the Museum of Comparative Zoology, 139(2):87-150. Harvard University.
- Mishler, B.D., and R.N. Brandon. 1987. Individuality, pluralism, and the phylogenetic species concept. *Biology and Philosophy* 2:397-414.
- Montanucci, R. 1969. Remarks upon the *Crotaphytus Gambelia* controversy (Sauria: Iguanidae). *Herpetologica* 25(4):308-314.
- . 1987. *A phylogenetic study of the horned lizards genus Phrynosoma, based on skeletal and external morphology*. Contributions in Science, no. 390, 36 pp. Natural History Museum of Los Angeles County.
- Montanucci, R., R. Axtell, and H. Dessauer. 1975. Evolutionary divergence among collared lizards (*Crotaphytus*), with comments on the status of *Gambelia*. *Herpetologica* 31(3):336-347.
- Norell, M.A. 1983. *Late Tertiary lizards from the Anza Borrego Desert*. San Diego: San Diego State University. Master's Thesis. 199 pp.
- . 1986. Late Pleistocene lizards from Kokoweef Cave, San Bernardino County, California. *Copeia* 1986(1):244-246.
- Norris, K. 1953. The ecology of the desert iguana *Dipsosaurus dorsalis*. *Ecology* 34(2):265-287.
- Olson, E. 1937. A Miocene lizard from Nebraska. *Herpetologica* 1:111-112.
- Opdyke, N., E. Lindsay, N. Johnson, and T. Downs. 1977. The paleomagnetism and magnetic polarity stratigraphy of the mammal bearing section of Anza Borrego State Park, California. *Quaternary Research* 7:316-329.
- Pappajohn, S. 1980. Description of Neogene marine section at Split Mountain, easternmost San Diego County, California. San Diego: San Diego State University. Master's Thesis. 77 pp.
- Peabody, F.E., and J.M. Savage. 1958. Evolution of a coast range corridor in California and its effects on the origin and dispersion of living amphibians and reptiles. *American Association for the Advancement of Science* 51:159-186.
- Pregill, G. 1981. *Late Pleistocene herpetofaunas from Puerto Rico*. Miscellaneous Publications, no. 71, 72 pp. University of Kansas Museum of Natural History.
- Presch, W. 1969. Evolutionary osteology of the iguanid lizard genus *Phrynosoma* (family Iguanidae). *Copeia* 1969:250-275.
- . 1970. The evolution of Macroteiid lizards (family Teiidae): an osteological interpretation. Los Angeles: University of Southern California. Dissertation.
- . 1974. Evolutionary relationships and biogeography of the macroteiid lizards (family Teiidae, subfamily Teiinae). *Bulletin of the Southern California Academy of Sciences* 73:23-32.
- Rage, J.-C. 1976. Les squamates du Miocène de Béni Mellal, Maroc. *Géologica Mediterrannée* 3:57-70.
- Ray, C. 1964. A small assemblage of vertebrate fossils from Spring Bay, Barbados. *Journal of the Barbados Museum and Historical Society* 31:11-22.
- Rickart, E. 1976. A new horned lizard (*Phrynosoma adinognathus*) from the early Pleistocene of Meade Co., Kansas, with comments on the herpetofauna of the Burchers locality. *Herpetologica* 32:64-67.
- Rieppel, O. 1980. The trigeminal jaw adductor musculature of *Tupinambis*, with comments on the phylogenetic relationships of the Teiidae (Reptilia: Lacertilia). *Zoological Journal of the Linnean Society* 69:1-29.
- Robinson, M.L., and T. Van Devender. 1973. Miocene lizards from Wyoming and Nebraska. *Copeia* 1973:698-704.
- Robinson, W., and W. Tanner. 1962. *A comparative study of the species of the genus Crotaphytus Holbrook (Iguanidae)*. Science Bulletin, Biological Series, no. 2(1), 31 pp. Brigham Young University.
- Rogers, K. 1976. *Herpetofauna of the Beck Ranch local fauna (Upper Pliocene: Blancan) of Texas*. Publications, Paleontological Series, no. 1(5), pp. 167-200. Michigan State University Museum.
- Savage, J.M. 1960. Evolution of a peninsular herpetofauna. *Systematic Zoology* 9(3):184-212.
- . 1963. *Studies on the lizard family Xantusiidae. IV. The genera*. Los Angeles County Museum Contributions to Science 71:1-30.
- . 1967. Evolution of the insular herpetofaunas. *Proceedings of the symposium on the biology of the California Islands*, ed. R.N. Philbrick, pp. 219-227. Santa Barbara: Santa Barbara Botanic Garden.
- Schatzinger, R. 1980. New species of *Paleoxantusia* (Reptilia: Sauria) from the Uintan (Eocene) of San Diego County, California. *Journal of Paleontology* 54:460-471.
- Schindel, D.E. 1980. Microstratigraphic sampling and the limits of paleontologic resolution. *Paleobiology* 6(4):408-426.
- Schoch, R.M. 1986. *Phylogeny reconstruction in paleontology*. New York: Van Nostrand, Reinhold. 353 pp.
- Setoguchi, T. 1978. *Paleontology and geology of the Badwater Creek area, Central Wyoming. Part 16. The Cedar Ridge local range (Late Oligocene)*. Bulletin no. 9, 61 pp. Carnegie Museum of Natural History.
- Smith, H. 1939. *The Mexican and Central American*

- lizards of the genus Sceloporus*. Field Museum of Natural History. Zoological Series 26:1-397, 31 pls.
- Stebbins, R. 1954. *Amphibians and reptiles of western North America*. New York: McGraw-Hill Book Company.
- Swinton, W. 1937. *Iguana* remains from Barbados. *Annals and Magazine of Natural History* 19:306-307.
- Taylor, E. 1941. Extinct lizards from the upper Pliocene deposits of Kansas. *State Geologic Survey of Kansas Bulletin* 38(5):165-176.
- Tihen, J.A. 1964. Tertiary changes in the herpetofaunas of temperate North America. *Senckenberg Biology* 45(3/5):265-279.
- Van Devender, T., and R. Eshelman. 1980. Referral of the fossil lizard *Sceloporus holmani* (late Pliocene of North Central Kansas) to the genus *Phrynosoma*. *Herpetologica* 35:380-382.
- Van Devender, T., and J. Mead. 1978. Early Holocene and late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. *Copeia* 1978(3):464-475.
- Van Devender, T., and R. Worthington. 1978. The herpetofauna of Howells Ridge Cave and paleoecology of the northwestern Chihuahuan Desert. In *Transactions of the Symposium of the Biological Resources of the Chihuahuan Desert region, United States and Mexico*, ed. R. Waver and T. Riskind. Washington, D.C.: National Park Service.
- Vanzolini, P., and J. Valencia. 1965. The genus *Draacaena*, with a brief consideration of macroteiid relationships (Sauria, Teiidae). *Arquivos de Zoologica de Estado de Sao Paulo* 13:7-35.
- Waddick, J., and H. Smith. 1974. The significance of scale characters in evaluation of the lizard genera *Gerrhonotus*, *Elgaria* and *Barisia*. *Great Basin Naturalist* 34:257-266.
- Weiner, N., and H. Smith. 1965. Comparative osteology and classification of the crotaphytiform lizards. *American Midland Naturalist* 73(1):170-187.
- Wellstead, C. 1982. Lizards from the Lower Valentine Formation (Miocene) of northern Nebraska. *Journal of Herpetology* 16(4):364-375.
- . 1983. *Leiocephalus nebraskensis* nom. nov. pro. *L. septentrionalis* Wellstead, 1982, a junior homonym. *Journal of Herpetology* 17(4):408.
- West, R. 1977. *Pleistocene geology and biology*, 2nd ed. London: Longman Group.
- Whistler, D.P. 1984. *An early Hemingfordian (Early Miocene) fossil vertebrate fauna from Boron, western Mojave Desert, California*. Contributions in Science, no. 355, 36 pp. Natural History Museum of Los Angeles County.
- White, J. 1969. Late Cenozoic bats (subfamily Nyctophilinae) from the Anza-Borrego Desert of California. *Contributions in Mammalogy—a volume honoring Professor E. Raymond Hall*. Miscellaneous Publications, no. 51, pp. 275-282. Kansas University Museum of Natural History.
- White, J., and T. Downs. 1961. *A new Geomys from the Vallecito Creek Pleistocene of California, with notes on variation on recent and fossil species*. Contributions in Science, no. 42, 34 pp. Natural History Museum of Los Angeles County.
- Woodring, W. 1931. *Distribution and age of the Tertiary deposits of the Colorado Desert*. Publications, no. 148, pp. 1-25. Carnegie Institute, Washington.

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